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Bulletin OF THE
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The Argyrolagidae, Extinct South American Marsupials

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CAMBRIDGE, MASSACHUSETTS, U.S.A.

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Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 15. (Price list on request.)

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Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

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THE ARGYROLAGIDAE, EXTINCT SOUTH AMERICAN MARSUPIALS

GEORGE GAYLORD SIMPSON

ABSTRACT

1. The known *Argyrolagidae* include two genera, for which the names *Microtragulus* and *Argyrolagus* are provisionally retained, with certainly four, possibly five or six valid species. *M. reigi* and *A. scagliai* are here described as new. The known range is mid or late Pliocene to early or mid Pleistocene in Argentina.

2. The dentition is $\frac{2\text{-}0\text{-}1\text{-}4}{2\text{-}0\text{-}1\text{-}4}$; incisors enlarged, procumbent below; all teeth rootless. The skulls have tubular bony snouts in advance of the incisors, a large, covered masseteric origin in the anterior part of the orbit, no distinct temporal fossa, and globular crania with somewhat inflated ear regions. Forelegs are reduced, hindlegs elongate; tibia and fibula are fused distally; metatarsals III and IV are appressed; there are only two digits in the pes; locomotion was bipedal ricochetal. The habitus is remarkably convergent toward some placentals, especially kangaroo rats and jerboas.

3. Argyrolagids are marsupials but show no clear affinity with any others known. They probably arose from didelphids independently of other known families and are distinct at the superfamily level, at least.

4. Although early steps in argyrolagid ancestry and specialization are unknown, they probably became differentiated in South America, and there is no evidence or present reason to postulate that they have ever occurred elsewhere. They do not indicate direct or indirect connection with Australia or the presence of a Southern Hemisphere bridge or intervening land.

5. Argyrolagids represent a distinct ecological habitus also found among independently evolved placentals in North America, Africa, Asia, and Australia (there also placental, not marsupial). The living animals of this habitus are characteristic of, although not confined to, deserts. The argyrolagids probably evolved also in adaptation to more or less local desert habitats, although the few specimens so far found were apparently not living under true desert conditions but marginally, in areas perhaps semiarid but not fully arid.

6. Argyrolagids (along with necrolestids and groeberiids) demonstrate that marsupial radiation in South America was even wider than indicated by the four families, Didelphidae, Borhyaenidae, Caenolestidae, Polydolpidae, usually considered in this connection. Prior to Pliocene-Recent invasions, all South American carnivores were marsupials, all medium to large herbivores were placentals, and other ecological niches were divided between placentals and marsupials, some of the latter, such as the argyrolagids, having extreme adaptive specializations. Marsupial radiation was almost as broad and reached almost as great extremes in South America as in Australia, the most important over-all difference being that in the latter continent the medium to large herbivores were marsupials.

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INTRODUCTION

The Argyrolagidae, also sometimes called the Microtragulidae, have been known after a fashion since 1904. After a fashion, only, for something has been lacking in knowledge of animals that have been considered rodents, ruminant artiodactyls, lagomorphs, notoungulates, diprotodont marsupials, paucituberculate marsupials, and polyprotodont marsupials, each after sober consideration by a qualified vertebrate paleontologist. That confusion had several causes. First, until the 1950's the animals were known only from isolated scraps. (The discoveries of the 1950's and later are here described for the first time.) Second, dissociated fragments, mainly metatarsals and mandibles, violated the Cuvierian "law" of association; it was impossible for a rational student to predict one part from another. Third, each part was decidedly *sui generis*, unlike anything else known. And fourth, in spite of that uniqueness, each part had certain (convergent, as we now know) broader similarities to various unrelated groups of mammals.

It is now possible to bring much, although not yet quite complete, order out of that confusion. First, skulls, mandibles, and considerable parts of skeletons are now known. Second, indubitable association can now be established among the diverse anatomical parts. Third, the oddity of the group is enhanced rather than lessened by these discoveries, but that makes its definition all the sharper. Fourth, it has thus become possible to identify most merely convergent resemblances as such.

There thus comes clearly into view, after all those years, a fascinating and absolutely unique group of marsupials that has evolved in a direction unlike any other marsupials or indeed any other mammals in South America, and yet in doing so has occupied ecological niches resembling those of unrelated, or only distantly related, groups elsewhere in the world. On this and other evidence, it is also becoming increasingly evident that marsupial radiation in South America was considerably more complex that has been generally realized. That, in turn, raises interesting evolutionary and biogeographical problems.

All of the measurements, in text and tables, are given in millimeters. In the tables L=length and W=width. The following abbreviations are used:

MMMP, Museo Municipal . . . de Mar del Plata (full name noted below).

MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (also known, e.g. in publication by L. Kraglievich, as the "Museo Nacional"), Buenos Aires.

ACKNOWLEDGMENTS

The discoveries that now add so enormously to our knowledge of this family were all made in the Chapadmalal-Miramar region, along the shore line exposures between Punta Mogotes and Punta Hermengo (southwest of Mar del Plata) under the auspices of the Museo Municipal de Ciencias Naturales y Tradicional de Mar

del Plata, Buenos Aires Province, Argentina. Most of the discoveries were made personally by Galileo Scaglia, Director of that Museum. Sr. Scaglia has made all the pertinent materials of that museum available for this study and has supplied excellent, detailed field data for each specimen. The very possibility of this work, along with its details of field occurrence, is thus due to him. Osvaldo Reig worked for a time in collaboration with Sr. Scaglia and also found some of the specimens here described. More recently he had planned to describe these materials himself, and, although he had not yet compiled any notes or manuscript, a number of illustrations in various stages toward completion were made under his direction. When he left Argentina to go first to the United States and then to Venezuela, he found it impossible to continue that research. He then most generously turned it over to me, arranging for delivery to me of the specimens, and also placing his illustrations at my disposal. I urged Dr. Reig to let his name appear as co-author of this monograph, but he firmly declined on the grounds that he would be unable to do any of the actual research. It must nevertheless be recorded that the study would not have been made by me or at this time if it had not been for Dr. Reig. Bryan Patterson had also long been interestd in these materials, and it was hoped for a time that he might undertake their study either alone or with me, but he waived his prior rights and insistently transferred the research to me.

Sr. Carlos Rusconi kindly supplied information on the type of *Argyrolagus parodii* Rusconi and gave me two unpublished photographs of that specimen. For functional comparisons data were provided by Dr. William D. Turnbull, Field Museum of Natural History, and Dr. Richard G. Van Gelder, American Museum of Natural History. The latter also provided a dipodid skeleton. Other specimens for comparison have been made available in the division of mammals of the Museum of Comparative Zoology, Harvard University, and from the zoological collections of the Department of Biology, University of Arizona. Drawings are by RaVae Marsh.

Most of this study was carried out under professorships, half-time each, in the Museum of Comparative Zoology, Harvard University, and the Department of Geology, University of Arizona. This monograph is a joint contribution from these institutions.

CLASSIFICATION

Superfamily Argyrolagoidea

The only known members of this taxon are the Argyrolagidae. It is sufficiently characterized by the diagnosis of that family and description of its members that follow. Justification for ranking as a superfamily is given in a later section on affinities.

Family Argyrolagidae Ameghino, 1904

Argyrolagidae Ameghino, 1904, vol. 58, p. 255.
Microtragulidae Reig, 1955, p. 61.

Type. Argyrolagus Ameghino, 1904.

Referred genus. Microtragulus Ameghino, 1904.

Known distribution. Late (possibly middle) Pliocene to early (possibly middle) Pleistocene, "Araucanian" to San Andrés Formation, Argentina.

Diagnosis. Small marsupials with dental formula $\frac{2.0.1.4}{2.0.1.4}$. Teeth hypselodont, rootless. Upper incisors recumbent and lower procumbent, forming a pinching apparatus. Presumed premolars small, nearly styliform. Upper molars simple, rounded lingually and flattened labially. Lower molars bilobed, anterior lobe larger, separation of lobes definite labially but may be obscure or absent lingually. Rostrum projecting well anterior to palate and incisors. Enormous palatal vacuities. Cranium inflated, with epitympanic and bullar cavities. Mandible with small coronoid process

relatively low condyle, and inflected angle. Anterior limbs small. Three main segments of posterior limbs greatly elongated. Only two functional metatarsals and toes. Locomotion probably ricochetal.

Generic and family nomenclature. Ameghino proposed the then new generic and specific names *Microtragulus argentinus* and *Argyrolagus palmeri* in the same paper (Ameghino, 1904). That paper was distributed as a unit with serial pagination, but its original publication was in six different installments extending over three volumes of a journal. The two genera and species were published in the same volume and year, but *Microtragulus argentinus* was in an earlier issue and therefore has definite temporal, and not only page, priority.

In the original publication, *Microtragulus* was referred to the artiodactyl family Tragulidae, with which it has nothing to do as is now evident, although the misinterpretation was almost inevitable at the time. The type and then only species was based on a supposed cannon bone, apparently fused metatarsals, which are indeed similar to those of some advanced artiodactyls. *Argyrolagus*, its type based on a mandible obviously not artiodactyl but somewhat rodentlike, was made the sole member of a then new proposed family Argyrolagidae. Until 1955 no other name for a family including either of these generic names was proposed. Rusconi (1936) suggested that *Argyrolagus* and *Microtragulus* are synonymous, but he did not note that in that case *Microtragulus* would have priority, and he continued to use the names *Argyrolagus* and Argyrolagidae. Reig (1955, 1958) indicated *Argyrolagus* as a junior synonym of *Microtragulus* and used the family name Microtragulidae. No explanation was given, but it was evident (and has been confirmed in personal communication) that *Microtragulus* was considered as a senior synonym of *Argyrolagus* and therefore the valid name for what was believed to be the sole genus of the family. The family name was changed to accord with the only supposedly valid generic name. That common sense procedure was then usual and was not contradicted by any rule or usage, although it has since been modified, contrary to common sense or earlier usage, by the Code of Nomenclature later promulgated (Stoll *et al.*, 1961, revised 1964).

There has been no first-hand study of this group since Rusconi (1933, 1936). Romer (1966, p. 379) listed it as "?Microtragulidae, *Microtragulus* [*Argyrolagus*]" (square brackets in the original). Rusconi (1967) continued to use the name Argyrolagidae, appearing somewhat less positive that *Argyrolagus* and *Microtragulus* are synonymous and continuing to ignore the fact that *Microtragulus* has priority. He again tentatively puts forward that synonymy and does recognize that priority in later personal communication.

The situation, never clear, is now further obscured by the fact that there are definitely two genera and at least four species, possibly as many as six, among the known specimens. One cannot therefore simply take it that *Microtragulus* is a senior synonym of *Argyrolagus* and decide the family name on that basis, a decision that would be equivocal enough under the peculiar provisions of the current code. That two genera exist is established on the basis of mandibles and lower dentitions, none of them from the same locality or horizon as the types of *M. argentinus* and *A. palmeri*. One of these genera known from other materials does, in all probability, include *A. palmeri*. The problem at the generic level is that it is unknown whether *M. argentinus* also belongs to that genus, in which case *Argyrolagus* is a synonym of *Microtragulus*, or whether it belongs to the other genus known from mandibles from other horizons and localities, in which case both *Microtragulus* and *Argyrolagus* are valid names.

A direct and positive solution to this problem will require finding metatarsals

clearly referable to *M. argentinus* and a mandible of the same individual. The mandible presumably would then indicate whether the type of *M. argentinus* is or is not congeneric with the mandible type of *A. palmeri* and whether it does or does not belong to the second genus known from dentitions. One may hope for such a solution but cannot reasonably expect it in the near future, at least—well over sixty years have elapsed without the production of a single scrap of an argyrolagid, let alone associated skull and limb bones, from the type deposit of *Microtragulus* and *Argyrolagus.*

In the meantime, only quite indirect comparisons are possible. Metatarsals are known from only one individual of this family aside from the type of *M. argentinus.* Fortunately in that one instance, MMMP No. 785-S, from the Chapadmalal formation, the bones are individually associated with a mandible. The mandible is considered congeneric but not conspecific with the type of *A. palmeri.* The metatarsals of that individual are morphologically like the type *M. argentinus* but are 25 per cent larger, a difference not impossible but improbable within a single species.

The second genus now known to belong to this family (whatever names may be given to the genera and the family) occurs at an "Araucanian" horizon probably earlier and almost certainly not later than Ameghino's types from Monte Hermoso, and also in the Chapadmalalan to the San Andrés formations in the Chapadmalal-Miramar region, beds younger than Monte Hermoso. Hence that genus must also have existed in Monte Hermoso time. The known specimens of jaws and cheek teeth are all definitely smaller than those of *A. palmeri* and others considered congeneric with the latter, including MMMP No. 785-S. Hence there is at least a possibility that the small metatarsals, type of *M. argentinus,* belong to the second genus (i.e. not to be the same genus as *A. palmeri*), for which *Microtragulus* would then be the valid generic name.

In MMMP No. 785-S the ratio of the length of the metatarsals to the length of M_{1-4} is 4.19. If the ratio were the same in an individual represented by a lower dentition from the San Andrés Formation (MMMP No. 960-M) belonging to the second genus, its metatarsals would be 26.4 mm in length. The length of the type *M. argentinus* is 28.5, only 9 per cent longer. Such little cogency as this very incomplete, very indirect comparison has, is, however, still further reduced by the facts that the San Andrés and Monte Hermoso individuals are quite unlikely to be conspecific, if only because there is a considerable difference in age, that they might well have had different limb-tooth proportions, and that similarity in length of metatarsals is not in any case a convincing generic character.

There is no possible objective solution to this problem. Any definite choice as to recognition and naming of the taxa at present must be purely arbitrary. Most clear-cut would be the tempting solution of having all the previous generic and family names officially rejected and then starting anew. In fact, the specific names, as will soon appear, are hardly in better shape and might be included in the holocaust. However, so radical an action is not likely to be accepted by the International Commission, would require long and costly argument and action, and even if officially approved, would be personally condemned by many zoologists.

I therefore propose action no less arbitrary but more conservative. I shall *assume,* until and unless contrary evidence is discovered, that the type of *Microtragulus argentinus* belongs to my "other genus" including *"Argyrolagus" catamarcensis* Kraglievich and MMMP No. 960-M (named *Microtragulus reigi* on a later page). On that assumption, *Microtragulus* is not synonymous with *Argyrolagus.* This

arbitrary assumption has these advantages:

It validates both of Ameghino's classic names for current continued usage, avoiding the necessity of coining any new generic names.

It validates the prior (by 51 years) family name and avoids a choice between family names that would be equivocal or insoluble under the current Code.

Nothing is known in definite contradiction of this usage. A final objective settlement, if one is ever achieved, is as likely to support this usage as to upset it. The chances are that any change that may later become necessary will be as slight under this usage as under any other.

Specific nomenclature. The status of the various previously proposed and here new specific names will be more particularly discussed under the following generic and specific headings. Here it may be pointed out in a more general way that this also is a problem that cannot at present be satisfactorily solved and can only be treated in a somewhat arbitrary way.

Four specific names have previously been proposed: *Microtragulus argentinus* Ameghino, 1904; *Argyrolagus palmeri* Ameghino, 1904; *Argyrolagus catamarcensis* Kraglievich, 1931; and *Argyrolagus parodii* Rusconi, 1933. The type of the first is not comparable with any of the others among these types. It is directly comparable with only one other known specimen, from which it differs specifically, at least. Indirect comparisons at the specific level are practically worthless. The type of *A. palmeri* is not at hand, although it may still be in existence. Available figures and descriptions of it seem to be adequate for comparison. The type of the last named species, *A. parodii*, has been virtually destroyed and available data are inadequate. Only for "*Argyrolagus*" *catamarcensis*, which proves to be a valid species but not to belong to *Argyrolagus*, is an adequate type actually in hand. In the collections here first described there are two clear-cut genera and species. The species are distinct from "*A.*" *catamarcensis* but one is considered congeneric with the latter. Comparisons of the species with *M. argentinus*, *A. palmeri*, and *A. parodii* are unsatisfactory and inconclusive because of the noted deficiencies of these types. I have more or less arbitrarily given new names to the fully definable and distinctive species in the new collection. As previously noted, I have with even greater arbitrariness here assigned Ameghino's two generic names to the two genera recognized in the hitherto undescribed materials.

The facts that the teeth are continuously growing and that the sequence of size is also a morphological sequence (see Figure 1) suggest the possibility that the apparent generic and specific distinctions are in fact merely functions of individual age in a smaller number of taxa, perhaps even in one species. The possibility cannot be absolutely ruled out, but it is quite improbable. The larger species have more, and more distinct, vertical grooves (or flexids) on the lower molars, whereas it is a rule with few, perhaps no, exceptions in mammals that these tend either to disappear or to become fossettids with increasing age (wear). There are certain other structural differences, such as the proportions of trigonid and talonid lengths, that are not likely to change individually in just this way. Size differences in lower jaws are not associated with other evidence of individual age differences. In all known specimens M_4^4 have erupted and are worn. Teeth measurable at the wear surface and the alveolar end are not distinctly larger at the latter end. Limb bones with fused epiphyses are of markedly different sizes, indicating that size differences are not in all, if in any, instances caused by growth. The apparently different species are in part from different geological horizons.

Distribution: The known distribution of named taxa is as follows:

Chapadmalal-Miramar area, Buenos Aires Province	Monte Hermoso, Buenos Aires Province	Catamarca Province
San Andrés Formation: *Microtragulus reigi*		
Barranca de los Lobos Formation: *Microtragulus reigi*		
Vorohué Formation: *Microtragulus reigi*		
Chapadmalal Formation: *Microtragulus reigi* *Argyrolagus scagliai*		
	Monte Hermoso Formation: *Microtragulus argentinus* *Argyrolagus palmeri*	
		?Andalhualá member or formation (in the "Araucanian"): *Microtragulus catamarcensis*

The exact level of ?*Argyrolagus parodii* is unknown. It is probably from either the Chapadmalal or the Vorohué Formation and is surely from within the indicated Chapadmalal-Miramar sequence.

The Chapadmalal Formation, as restricted by Kraglievich (1952), is probably basal Pleistocene in age, now that Blancan in North America and Villafranchian in Europe are generally considered Pleistocene rather than Pliocene as sometimes earlier designated. The three overlying formations in which argyrolagids occur do not seem to cover any considerable span of time and are probably also early Pleistocene but could just possibly extend into the middle Pleistocene. Actual superposition of Chapadmalal on Monte Hermoso has not been demonstrated, but Monte Hermoso is generally considered somewhat older, and hence Upper Pliocene, on faunal grounds. "Araucanian" is an obsolescent and inappropriate name for a long sequence of mainly Pliocene beds. It seems to include strata of Monte Hermoso age, but also some distinctly older. The type of *M. catamarcensis* is labeled "Andalhualá," presumably for the locality, and may well be from the beds so named with that as type locality. If so, the age of this type is probably pre-Monte Hermoso and approximately middle Pliocene.

Genus *Microtragulus* Ameghino

Microtragulus Ameghino, 1904, vol. 58, p. 191.

Type. Microtragulus argentinus Ameghino.

Referred species. M. catamarcensis Kraglievich and *M. reigi*, new species.

Known range. Upper (or possibly Middle) Pliocene to Lower (or possibly Middle) Pleistocene, Argentina.

Diagnosis. (For reasons explained elsewhere, this diagnosis is arbitrarily based on the referred and not the type species.) M_{1-3} with rounded lingual faces, internal groove absent or slight, external groove present, relatively posterior, partially distinct second lobe short and wide. These teeth almost as wide as long. M_4 elongate, distinctly bilobed, second lobe narrow.

Discussion. The above characters, shared by *M. catamarcensis* and *M. reigi*, sharply distinguish those species from *Argyrolagus palmeri* and *A. scagliai*. The teeth are more fully described and other morphological distinctions are mentioned in the anatomical section of this study.

Microtragulus argentinus Ameghino

Microtragulus argentinus Ameghino, 1904, vol. 58, p. 191; 1906, fig. 344.

Type MACN No. 4743, metatarsals III-IV and associated tarsal bones.

Hypodigm. Type only.

Known range. Monte Hermoso Formation, Monte Hermoso, Buenos Aires Province.

Original diagnosis (of genus and species). "The smallest of known artiodactyls, since its size did not exceed that of a small rat. . . . The metatarsal or cannon bone, formed by the fusion of the two median metatarsals III and IV, is only 27 mm long and 2 mm wide in its narrowest middle part. . . . The two metatarsals in question . . . are fused for their whole length but between the two there remains a deep longitudinal groove in the anterior face and another, shallower, on the posterior face. The lateral metatarsals II and V are atrophied, represented only by their styliform proximal ends, this part of metatarsal V being fused with that of metatarsal IV, but that of metatarsal II remained separate. The cuboid, scaphoid [navicular], and cuneiforms are separate, but are constructed, like the other bones, on the same type as that of the Tragulidae."[1] (Parts of the diagnosis merely descriptive of *Hypisodus* and now known to be irrelevant are omitted.)

Discussion. The name is not known to be preoccupied, was the first ever applied to a member of this family, and was given a definition technically sufficient under the Code. It is therefore necessarily valid as a name. However, the diagnosis, which is relative to tragulids and to *Hypisodus* (a hypertragulid), placental artiodactyls, is simply irrelevant now that *Microtragulus* is known to be a marsupial. Direct comparison is possible only with the type of *Argyrolagus scagliai.* The metatarsals (not in fact fused) agree except that those of the latter are 25 per cent longer. The reasons for arbitrarily placing them in different genera, as well as species, have been given above. It is probable that *M. argentinus* was of approximately the size of *M. reigi,* with which direct comparison is impossible at present. I find the dimensions of the type (appressed metatarsals) of *M. argentinus* to be slightly larger than those given by Ameghino: 28.6 in length and 2.4 in (transverse) width at the narrowest point. The minimum anteroposterior diameter is 1.5.

Microtragulus catamarcensis (L. Kraglievich)

Argyrolagus catamarcensis L. Kraglievich, 1931, reprinted in L. Kraglievich, 1940, p. 592. (Not previously figured.)

Type. MACN No. 5529. Parts of both rami of the mandible with left I_1 and P_3-M_4 (poorly preserved), right I_1, and M_{1-3}, and other alveoli and fragments.[2]

Hypodigm. Type only.

Known range. Araucanian of Catamarca ("los yacimientos araucanenses de Catamarca"). A label with the specimen says, "Andalhualá Catamarca F. Araucana." Andalhualá is evidently named as at or

[1] "Es el más pequeño de los artiodáctilos conocidos, pues su tamaño no excedía al de una pequeña rata. . . . El hueso metatarsiano ó cañón formado por la fusión de los dos metatarsianos 3 y 4, solo tiene 27 mm. de largo y 2 mm. de ancho en su parte media más angosta. . . . Los dos metatarsianos en cuestión . . . están soldados en todo su largo, pero se conserva entra ambos un profundo surco longitudinal en su cara anterior y otro más superficial en la cara posterior. Los metatarsianos laterales 2 y 5 son atrofiados, representados tan sólo por sus extremidades proximales estiliformes, siendo esta parte del metatarsiano 5 soldada con la del metatarsiano 4, pero la del metatarsiano 2 se conservaba independiente. El cuboides, el escafoides y los cuneiformes se conservan independientes, pero construidos, como también los demás huesos, sobra el mismo tipo del de los Tragulidae."

[2] In the same vial there is a fragment of bone with a lower molar tooth apparently of *Carologameghinia mater,* a rare genus and species known only from the Casamayoran of Patagonia. There cannot be any connection between the two specimens.

near the locality where the specimen was found. It is also the type locality for a subdivision of the Araucanian beds, and there is some probability that the specimen came from that stratigraphic subdivision. It is shown, for example, on the correlation chart, pl. IV, of J. L. Kraglievich (1952).

Original diagnosis. No formal proposal or diagnosis was given, but, in the course of a discussion of *Argyrolagus palmeri,* L. Kraglievich gave this name as new,[3] with enough description to validate the name under the then existing code of nomenclature; from that discussion I have abstracted such comments as might have been considered distinctive of the species in comparison with *A. palmeri.*

"In the Araucanian deposits of Catamarca, somewhat older than that of Monte Hermoso, I have established the presence of another argyrolagid, which I shall call *Argyrolagus catamarcensis* n. sp., much smaller than *A. palmeri.* The animal is represented by a large part of the mandible (No. 5529, paleontological collection of the National Museum), with the body of both rami, the median incisors and several cheek teeth of one side or the other, of really tiny size but of a structure similar to the genotype species in every respect."[4] There follows a description not said to be and not in fact distinctive from *A. palmeri.* Then: "Perhaps the anterior accessory groove of the second cheek tooth [M_1] (the first preserved) is a little weaker than in *A. palmeri.* The anteroposterior diameter of the median incisor scarcely exceeds 1 mm. The maximum height of the rami below the cheek teeth does not reach 5 mm, and the three intermediate cheek teeth [i.e., the second to fourth or M_{1-3}] occupy a space of only 4 mm."[5]

Revised diagnosis. Smaller than *H. reigi;* M_{1-4} 31 per cent longer in type of the latter than in type of *H. catamarcensis.* Lingual groove absent on M_{1-3}. Measurements in Table 1.

Discussion. The brief new diagnosis suffices to distinguish this species from others in which the lower dentition is known. Further details are given in the discussion of anatomy. It is improbable that this name is synonymous with *H. argentinus.* The type metatarsals of the latter are probably too large for *H. catamarcensis,* and there is considerable difference in geological age.

Microtragulus reigi[6], new species

Type. MMMP No. 960-M, part of right mandibular ramus with all teeth. Collected by G. Scaglia at Punta San Andrés, San Andrés Formation.

Hypodigm. The type and the following: MMMP No. 714-S, part of left mandibular ramus with M_{2-4}; collected by O. Reig in

[3] This offhand presentation, buried in a text paragraph, doubtless explains why "*A.*" *catamarcensis* does not figure in the relevant bibliography, Camp and Vanderhoof (1940), which does cite the publication in which the name appeared.

[4] In fact the structure of these teeth is strikingly different from that of *Argyrolagus palmeri,* as is now shown. That an observer of L. Kraglievich's high caliber thought the structure the same is due to the fact that the outlines of the molars were obscured by matrix, which has subsequently been removed without damage to the specimen.

[5] " . . . en los yacimientos araucanenses de Catamarca, algo más antiguos que el de Monte Hermoso, he comprobado la presencia de otro argirolágido, que denominaré *Argyrolagus catamarcensis* n. sp., mucho más pequeño que *A. palmeri.* El animal está representado por una gran parte de la mandíbula (N° 5529, colec. paleont. Mus. Nac.), con el cuerpo de ambas ramas, los incisivos medios y varios molares de uno y otro lado, de un tamaño verdaderamente diminuto, pero de una conformación en todo similar a la especie genotipo. . . . Tal vez el surco accesorio anterior del m 2 (primero de los molares conservados) es un poco más débil que en *A. palmeri.* El diámetro anteroposterior del incisivo medio apenas pasa de 1 milímetro; la altura máxima de las ramas debajo de los molares no llega a 5 milímetros y los tres molares intermedios ocupan tan sólo un espacio de 4 milímetros."

[6] For Dr. Osvaldo Reig whose essential contributions to this study are acknowledged above.

a disgorged food pellet in the Atlantic coastal cliff 300 meters south of the Arroyo Lobería, Vorohué Formation, bed III. MMMP No. 691-S, nearly complete skull, lacking snout; collected by G. Scaglia at foot of cliff 120 meters south of the Bajada de las Palomas, Chapadmalal Formation, probably bed 3 or 4. MMMP No. 661-S, right maxilla with P^3-M^4; collected by G. Scaglia 500 meters south of Punta Vorohué, one meter above sea level, Barranca de los Lobos Formation. MMMP No. 395-M, fragments of maxilla and mandible, with limb bones and fragments of several (probably three) individuals, perhaps not all of this species; collected by G. Scaglia in the cliff 550 meters northeast of Arroyo Brusquitas, Barranca de los Lobos Formation, bed I. Some of the skeletal remains, not associated with teeth, listed and described under "anatomy" probably belong to this species, but only specimens with teeth are explicitly placed in the hypodigm.

Known range. Early Pleistocene (Chapadmalal to San Andrés formations) of the Chapadmalal-Miramar region, Buenos Aires Province. More precise localities and horizons of the known specimens given above.

Diagnosis. Larger than *M. catamarcensis.* M_{1-3} with shallow but definite lingual grooves. Measurements in Tables 1 and 2.

Discussion. No metatarsals that could be referred to this species are known from the beds in which the teeth of the hypodigm were found. Comparison with the type of *M. argentinus* is therefore impossible. The two nominal species are of about the same size, although a metatarsal somewhat smaller than the type of *M. argentinus* might be expected in *M. reigi.* The Monte Hermoso and Chapadmalal, *sensu lato,* faunas are largely different. Virtually no species are recorded as common to both, and L. Kraglievich's enumeration (1934) shows only 24.3 per cent of total then known and well-identified genera as present in both, although he indicated that 54.5 per cent of the well-identified genera of the smaller Monte Hermoso fauna are present in the (unrestricted) Chapadmalal. The specific distinction may well be exaggerated by the tendency to define nominal species as distinct just because the specimens in question are from different beds. Nevertheless, the Monte Hermoso fauna clearly is largely different from that of the Chapadmalal or any known later fauna. Reference of the Chapadmalal-San Andrés specimens to the Monte Hermoso species would go against some probability. A name is needed for these excellent and important specimens, and dubious reference to the earlier species would now be more misleading than reference to a new species, even though the name of the latter could conceivably later prove to be a synonym.

Genus *Argyrolagus* Ameghino

Argyrolagus Ameghino, 1904, vol. 58, p. 255.

Type. Argyrolagus palmeri Ameghino.

Referred species. A. scagliai, new species, and doubtfully ?*A. parodii* Rusconi.

Known range. Late Pliocene (Monte Hermoso) to early Pleistocene (Chapadmalal), Argentina.

Diagnosis. (Differential from the only other genus now recognized in the family, called *Microtragulus* by the arbitrary usage previously explained.) M_{1-4} strongly and definitely bilobed, with opposite labial and lingual vertical grooves of approximately equal strength; definitely longer than wide; second lobe relatively longer than in *Microtragulus.* M_4 not so markedly unlike M_3.

Discussion. The characters noted in the diagnosis sharply distinguish these species from those here designated as *Microtragulus catamarcensis* and *M. reigi.* Comparison with the genotype of *Microtragulus, M. argentinus,* is possible for *A. scagliai,* but indicates only that the metatarsals of the latter species are longer and stouter than those of the former. As previously explained, it is possible that the type of *M. argentinus* does belong to *Argyrolagus,* in which case *Argyrolagus* is a synonym of

Microtragulus, and the species here called *M. catamarcensis* and *M. reigi* do not belong to that genus. It is, however, at least equally plausible that a real generic distinction simply is not evident in the metatarsals. There are many examples among mammalian genera closely related but generally accepted as distinct in which the generic distinction is not evident in metatarsals or other limb segments. The resemblance does indicate close relationship and shows beyond serious doubt that *Microtragulus* and *Argyrolagus,* whether truly distinct genera or not, do belong in the same family.

Other characteristics of *Argyrolagus,* as here restricted, are given in the section on anatomy.

Argyrolagus palmeri[7] Ameghino

Argyrolagus palmeri Ameghino, 1904, vol. 58, p. 255; Ameghino, 1906, fig. 221; L. Kraglievich, 1931, fig. 2.

Type. Ameghino Collection, presumably in MACN but not seen, part of a left mandibular ramus with I_1, M_{1-4}, and alveoli of I_2 and P_3.

Hypodigm. Type only.

Known range. Monte Hermoso Formation at Monte Hermoso, Buenos Aires Province.

Original diagnosis (of genus and species). "Medial incisor narrow, flat on the internal and convex on the external side, as in *Prolagus;* the root of this incisor reaches only as far as below the fifth cheek tooth. The second incisor smaller, elliptical, located posterior to the medial incisor and separated from the following cheek tooth by a short diastema. The five cheek teeth in continuous series, the first elliptical and the following four composed of two prisms, all very long and with open roots. Horizontal ramus with a very convex ventral border. Length from the anterior part of the medial incisor to the posterior edge of the last cheek tooth 14.5 mm. Length of the space occupied by the five cheek teeth 9 mm."[8]

Revised diagnosis. About the size of *A. scagliai* or slightly smaller. Anterolabial projection of M_1 less pronounced. M_{1-3} narrower relative to length. Talonid of M_4 without posterior projection. Measurements derived from illustrations in Ameghino (1906) and L. Kraglievich (1931) are given in Table 1.

Discussion. Ameghino's original diagnosis or, rather, description was not differential, as there was then nothing to compare with. Even the supposedly related lagomorphs are all so obviously different that a diagnosis against them was unnecessary. Of course it has long since been recognized that this was because the groups are not, in fact, related. Although the specimens here grouped in *Microtragulus* are indeed related to *A. palmeri,* those with known lower dentitions (*M. catamarcensis* and *M. reigi*) are quite distinct, as indicated here by their generic

[7] The name was given in honor of the North American mammalogist T. S. Palmer, author of the *Index Generum Mammalium,* a work now sometimes maligned but still extremely useful and irreplaceable; indeed even now, as Ameghino wrote in 1904, "The most complete and perfect compilation of its sort ever written." It had just been issued when Ameghino wrote those words in a footnote to his description of this genus and species.

[8] "Incisivo interno angosto, plano sobre lado interior y convexo sobre el externo, igual al de *Prolagus;* la base de este incisivo sólo llega hasta debajo de la muela 5. Incisivo segundo más pequeño, elíptico, colocado detrás del incisivo interno y separado de la muela que sigue por una barra corta. Las cinco muelas en serie continua, la primera elíptica y las cuatro siguientes compuestas de dos primas [sic!], todas muy largas y de base abierta. Rama horizontal de borde inferior muy convexo. Longitud de la parte anterior del incisivo interno al borde posterior de la última muela, 14.5mm. Longitud del espacio ocupado por las 5 muelas, 9mm."

Ameghino designated all permanent postcanine teeth in mammals, premolars and molars of other authors, as molars; I therefore translate his "muela" as "cheek tooth." "Primas" is an obvious misprint for "prismas."

separation. *A. scagliai,* new here, is much closer to *A. palmeri,* but the characters indicated in the diagnosis adequately indicate specific distinction. The two are of definitely, although not greatly, different ages.

I have not seen the actual specimen, but the descriptions by Ameghino and especially by L. Kraglievich are detailed, and they agree well, as do their figures, three of which are given by Ameghino and two by L. Kraglievich. As shown in Table 1, measurements made on these figures (all of which are ×2), although differing by as much as 0.4 mm in extreme cases, are in sufficiently close agreement to be trusted as approximate, at least, when averaged.

Argyrolagus scagliai,[9] new species

Type. MMMP No. 785-S, nearly complete skull, left ramus of mandible, pelvis and sacrum, right and left femora, right and left tibiae and fibulae, right and left metatarsals, partial right and left tarsi, part of scapula, partial right and left humeri, vertebrae, and various fragments; collected by G. Scaglia, 200 meters north of the Bajada de los Lobos, Chapadmalal Formation, bed 9.

Hypodigm. Type and the following: MMMP No. 741-M, part of right mandibular ramus with all teeth; from the Bajada las Palomas, Chapadmalal Formation, bed 9. MMMP No. 802-M, most of skull, lacking snout; from Punta Plataforma, Chapadmalal Formation. MMMP No. 281-S, partial left side of skull; collected by G. Scaglia 100 meters south of the Bajada de la Barranca de los Lobos, Chapadmalal Formation, bed 9. MMMP No. 973-M, most of palatal and adjacent facial parts of skull with all teeth except right I^1; collected by G. Scaglia at Vivero, Arroyo Lobería, Chapadmalal Formation, bed 8. MMMP No. 974-M, part of left ramus with P_3-M_2; collected by G. Scaglia on the south side of Arroyo Brusquitas, Chapadmalal Formation, bed 9. Some of the skeletal parts mentioned in the section on anatomy may also belong to this species, but they are not formally included in the hypodigm.

Known range. Chapadmalal Formation, early Pleistocene, of the Chapadmalal-Miramar region, Buenos Aires Province. Details given above. (By what is probably coincidence, all the identified specimens of exactly known level are from beds 8 and 9 of the Chapadmalal, relatively high levels in that formation.)

Diagnosis. About the size of *A. palmeri* or slightly larger. Pronounced anterolabial projection on M_1. M_{1-3} relatively wide (more than in *A. palmeri,* less than in *Microtragulus*). M_4 talonid relatively complex, with posterior projection.

Discussion. This, now much the best-known species of the family, is described in detail in the section on anatomy.

?*Argyrolagus parodii* Rusconi

Argyrolagus Parodii Rusconi, 1933, p. 245, figs. 1 and 10; 1936, figs. 6b, 9, 10, and 12.

Type. Part of a left mandibular ramus with M_{3-4}. This was collected by Lorenzo W. Parodi, apparently on his own and not for a museum or other institution. He turned the specimen over to Carlos Rusconi, who has informed me (letter of 24 October 1967) that the specimen "is in my possession (in my house), but unfortunately someone has broken it and it is in small bits. I do not know whether it can be reconstructed."[10] Evidently comparisons are now impossible, and Sr. Rusconi did not think it worth while to forward the remaining fragment or fragments for comparison.

[9] For Galileo Scaglia, who collected many of the specimens here described, who made them all available, and who supplied the data on localities and levels.

[10] " . . . se halla en mi poder (in my house) [parenthetical expression English in the original]. Pero, desgraciadamente alguna persona me la ha roto y se encuentra en pequeños trozos. Ignoro si podría ser reconstruida." Rusconi then adds in English, "(This mandibular fragment in [is] broken or destroyed but [I] preserve some fragment.)"

Table 1. Measurements of Lower Teeth of Argyrolagidae

	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W	M_4 L	M_4 W	LM_{1-4}	LM_3/LM_4	LM_3/WM_3
Microtragulus											
M. catamarcensis, type	1.2	0.8	1.2	1.2	1.2	1.0	1.1	0.7	4.8	1.09	1.20
M. reigi, type	1.6	1.3	1.6	1.4	1.7	1.6	1.5	1.1	6.3	1.11	1.06
MMMP No. 714-S	–	–	1.5	1.5	1.5	1.4	1.4	0.9	–	1.07	1.07
Argyrolagus											
A. palmeri, type											
From Ameghino, 1906,											
Fig. 221a	1.8	1.1	1.9	1.3	2.0	1.3	1.7	1.2	7.5	1.18	1.54
Fig. 221e	1.9	–	1.9	–	2.1	–	1.9	–	7.6	1.10	–
Fig. 221o	2.0	–	2.1	–	2.0	–	2.0	–	7.8	1.00	–
From Kraglievich, 1931											
Fig. 2, upper	1.7	1.1	1.9	1.3	2.0	1.3	2.0	1.1	7.7[a]	1.00	1.54
Fig. 2, lower	1.6	–	2.2	–	2.4	–	2.0	–	7.7	1.20	–
Mean of five preceding[b]	1.8	1.1	2.0	1.3	2.1	1.3	1.9	1.15	7.66	1.10	1.62
A. scagliai, type	1.7	1.4	2.0	1.7	2.0	1.6	2.2	1.2	8.5	0.91	1.25
MMMP No. 741-M	2.1	1.9	2.3	1.8	2.1	1.8	2.2	1.3	8.4	0.95	1.17
MMMP No. 974-M	2.0	1.8	2.3	2.0	–	–	–	–	–	–	–
?*A. parodii*, type											
Rusconi, 1933, text	–	–	–	–	1.9	–	1.3	–	–	1.46	–
Rusconi, 1933, fig. 1a	–	–	–	–	1.8	1.6	1.6	1.2	–	1.12	1.12
Rusconi, 1936, fig. 12	–	–	–	–	1.6	1.4	–	–	–	–	1.14

[a] Kraglievich gives 7.5 in the text.

[b] This is a mean of the five sets of measurements derived from different illustrations of the same specimen; it is not a mean of five specimens or five independent measurements.

Hypodigm. Type only.

Known range. This specimen was found and described before J. L. Kraglievich and his associates had restricted the Chapadmalal Formation and given new names to overlying beds. It was published (Rusconi, 1933) as from "Miramar, province of Buenos Aires; *Chapadmalense* beds, Middle Pliocene." In reply to my enquiry as to whether any more precise data are available, Rusconi kindly replied, "This type specimen, according to friend Parodi, was found by him in the Chapadmalalan? terrain, between the localities Las Brusquitas and Vuelta Mala, on 30 January 1932. Nevertheless it is possible that the exact level of the fossil may have been between the Post-Chapadmalalan and the Ensenadan. I do not know personally the exact spot from which said specimen comes."[11] Vuelta Mala is not indicated on maps available to me, but there is an Arroyo las Brusquitas approximately 5.7 kilometers northeast of the center of the town of Miramar, and J. L. Kraglievich (1952, plates I and II) indicates a Barranca Parodi a short distance southwest of the mouth of that arroyo. The specimen in question doubtless came from that general region. According to J. L. Kraglievich, the only beds exposed within several kilometers of there are the Chapadmalal,

[11] "Esta pieza tipo, según el amigo Parodi, la encontró en terreno chapadmalense?, entre las localidades de las Brusquitas y Vuelta Mala, Enero 30 de 1932. Sin embargo puede ser que el nivel justo del fósil haya sido entre el Post-chapadmalense y el Ensenadense. Yo, personalmente, no conozco el lugar exacto de donde procede dicha pieza."

Vorohué, and Lobería formations. The Lobería is latest Pleistocene or Recent and it is highly improbable that the specimen came from it. The specimen almost certainly came from the Chapadmalal, *sensu stricto,* or from the immediately succeeding and hardly appreciably later Vorohué. Its age according to most present usage is therefore early Pleistocene.

Original diagnosis. A separate, formal diagnosis was not given; I have extracted from the extended description specifications of characters evidently considered diagnostic. The original publication is in English, translated by Violeta Lelong from the author's Spanish manuscript.

"Ascending ramus lower than that of *Argyrolagus palmeri,* but somewhat larger than that of the *A. catamarcensis* Kragl. . . . Between M_3 [i.e., the last cheek tooth, M_5 of Ameghino and L. Kraglievich, M_4 of usual notation for marsupials] and the coronoid crest there is an excavated surface that is placed in an oblique direction and in whose bottom there is a vertically descending hole that communicates with the posterior dental foramen. . . . This canal apparently does not exist in *A. palmeri.* . . . The anterior margin of the coronoid crest of *A. palmeri* is inclined obliquely downward. It describes a feeble curve and terminates at the level of the penultimate molar. The corresponding margin of *A. parodii,* on the contrary, ends in a strong, bony edge, bent downward nearly at a right angle, and behind it there appears an irregular and rather characteristic depression. . . . The inferior mandibular edge in the new species, principally from the level of the penultimate molar backwards, is straighter than it is in *A. palmeri.* There is some difference between the two hinder molars, but the most important is the slightly greater thickness of M_3 [M_4] as compared with the penultimate molar. In *A. palmeri* these teeth are of nearly equal size."

Tentative revised diagnosis. M_3 about the size of *A. palmeri* and *A. scagliai,* but relatively wider, talonid lobe shorter, buccal and lingual grooves opposite, subequal. M_4 with second lobe more distinct, less narrowed than in *Microtragulus catamarcensis* but more narrowed than in *Argyrolagus palmeri* and *scagliai.*

Discussion. As the type has been virtually if not literally destroyed and no other specimens surely conspecific are known, judgment must now be based on Rusconi's description and figures and on two unpublished photographs, one in labial and the other in lingual view, kindly sent to me by Rusconi for this study. These photographs, scale not indicated but probably about ×1½, do not agree in detail with Rusconi's published figures, and when they were taken the specimen apparently had already suffered some breakage although it had not yet been reduced to fragments.

The three views in Rusconi (1933, fig. 1) are marked "×2" but according to Rusconi's measurements (p. 250), that is approximately correct for figure 1a, only. The scale of 1b and 1c (assuming the table of measurements to be nearly correct) is approximately ×1½ Rusconi gives 1.9 and 1.3 as the lengths of M_3 and M_4 (his "M_2" and "M_3") respectively. If these figures are correct, M_3 is near the size of *Argyrolagus palmeri* and *A. scagliai* but M_4 is at least as small as in *Microtragulus reigi.* The ratio LM_3/LM_4 on these figures is 1.46, much larger than in any other known specimen of this family, and that may be a distinction of the species. However, if we accept figure 1a as being × 2, the two lengths measured thereon are 1.8 and 1.6, the ratio 1.12, which is within the range for both *M. reigi* and *A. palmeri.* (See Table 1.)

The crown view, figure 1a, in Rusconi's first paper (1933) seems to differ considerably from that, figure 12, in his later discussion (1936). If the former is correct, this tooth would appear to have a deeper lingual groove than any other M_3 known in the family and to have this posterior to

the labial groove, not opposite the latter. Such a structure would be highly distinctive. However, the later figure is clearer and is also drawn to a larger and apparently more accurate scale. I have therefore assumed it to be correct, an assumption that cannot be checked until other specimens of this species are found. On this assumption, M_3 resembles *Argyrolagus* in having subequal labial and lingual grooves but *Microtragulus* in having a short talonid. The distinction and narrowing of the talonid of M_4 is approximately intermediate between those genera, in species more definitely referred to them. It is thus quite unlikely that ?*A. parodii* is synonymous with any other, earlier or later, specific name. Generic reference is uncertain, but the later figure of M_3 (Rusconi, 1936, fig. 12) is perhaps nearer to *Argyrolagus* than to *Microtragulus.*

The other characters given by Rusconi are not distinctive. The statement that the ascending ramus is lower in his type is puzzling, because the height of that part was not determinable in that specimen or any other of this family available for comparison. The vertical canal posterior to the molars is present in all specimens of the family in which this region is preserved. L. Kraglievich (1931) had already noted its presence in *A. palmeri.* The ridge and depression on the buccal side of the ramus are also normal for the family, but they vary in degree of prominence. In Rusconi's type they do seem to be more prominent than in some specimens, yet not uniquely so. This might be a character of sex or of individual age. The apparent difference in curvature of the ventral border of the ramus, slight in any case, is largely if not wholly an effect of the way in which the specimen is broken and dependent on what was accepted as a normal horizontal. The latter is also the cause of the supposed peculiarity, discussed by Rusconi at length and subject of extended pictorial comparisons (Rusconi, 1933, figs. 2–11) that the condyle is below the level of the alveolar border. The error was natural at the time, but now that more complete jaws are known it is seen that the border is rising posteriorly under M_{3-4} and there is not indicative of a true horizontal. When the whole alveolar border is taken into consideration, the condyle is above its level. This effect can be seen in Rusconi's figure (1933, fig. 4) of the mandible of *Paraepanorthus* (a caenolestid). If the line "X" indicating the level of the alveolar border in *Paraepanorthus* were drawn from M_{3-4} only, the condyle would be well below it, not above it as (correctly) shown. It follows that Rusconi was also mistaken in deducing that the glenoid cavity of the skull of his specimen of *Argyrolagus* must have been beyond (i.e., below) the level of the triturating surface of the upper molars. (See section on anatomy later in this study.)

ANATOMY

Dentition. The following description of the dentition is based primarily on *Argyrolagus scagliai* and especially on the type of that species, MMMP No. 785-S. Notable divergences from that species and specimen are noted. Striking differences believed to be of taxonomic importance have been incorporated in preceding diagnoses of taxa.

Each side of each jaw, upper and lower, has two gliriform-incisiform anterior teeth. Those in the upper jaw are in the premaxilla and are therefore incisors. Those in the lower jaw are also almost surely incisors. Their homologies among the more numerous ancestral incisors are not surely determinable, but the more anterior are nearly medial in position, and the next follow without diastemata. It is therefore plausible, at least, that these teeth are I_{1-2}^{1-2}, and in any case they can be so designated for purposes of description. They are followed in each jaw by a prominent diastema and then by five cheek teeth in closed sequence. The first of these, although not strictly styliform

as previously described (for the lower dentition), are distinctly unlike those following and are simpler in structure. The other four teeth, with some differences among themselves, form a graded, molariform series. The available specimens show no evidence of tooth replacement. The homologies of these cheek teeth with the longer ancestral sequence are, again, not strictly determinable, but it is plausible that they are homologous with the teeth usually designated $P^{3}_{3}M^{1-4}_{1-4}$ in marsupials.[12] The conventional dental formula is therefore adopted as $\frac{2.0.1.4}{2.0.1.4}$ and provisionally homologized as $I^{1-2}_{1-2}\, P^{3}_{3}\, M^{1-4}_{1-4}$. Although this is convenient for purposes of description, the homologies of I^{1-2}_{1-2} in this family are uncertain with respect to other marsupials, and the teeth almost always designated P^{3}_{3} in marsupials may be incorrectly numbered by ancestral homologies.

As far as determinable, all teeth are completely hypselodont, continuously growing. In MMMP No. 661-S postmortem erosion has laid open the dorsal ends of the crypts of the upper cheek teeth. Although all of these have erupted and are worn, the pulp cavities are wide open and there is no sign of the formation of roots. The corono-basal length of M^2 is 7.3, which is 4.3 times the anteroposterior length of the crown. The corono-basal length of the other cheek teeth is somewhat less. These teeth certainly continued to grow for a long time, and probably did so continuously throughout the life of the animal. No specimen, as now prepared, positively demonstrates this for the incisors, but it is highly probable for them as well.

I^1 is a large tooth, somewhat curved (convex anteriorly) in the corono-basal direction. The mouths of the alveoli of left and right I^1 are slightly separated, but the curvature and implantation of the teeth are such that their working faces are in contact medially. Each tooth is triangular in cross section, with each of the three sides slightly curved. Longest is the flattened labial face. The medial point is the apex of the triangle. The short side is postero-labial (or distal) and abuts against I^2. The exposed part of I^1 is recumbent and works against the end of strongly procumbent I_1. On both I^1 and I^2 the labial face is well enameled, but enamel is thin or possibly absent on the lingual face. I^2, somewhat larger than I^1, is slightly procumbent. Its anterior (or mesial) tip lies against the tip of I^1. The cross section is that of a long, thin oval or tear drop, the broader end anterior, the thin, following (posterior, distal) end almost angular.

Nominal P^3 is a small, comparatively simple tooth, somewhat recumbent so that it is tightly appressed against the middle of the anterior (mesial) face of M^1, immediately lingual to its parastylar lobe or projection. The cross section of P^3 is long subovate or subtriangular, the blunt end posterior.

In *A. scagliai* M^1 is abruptly larger than P^3; M^2 is still larger, M^3 about the size of M^1, and M^4 slightly smaller than M^{1-3} but still larger than P^3. In *M. reigi* there is little difference in size in M^{1-3} but M^4 is markedly smaller, relatively more so than in *A. scagliai*. These differences are evident in Table 2. In both genera and species M^{1-3} are somewhat flattened on all four of the more or less vertical faces, and hence are subquadrate. Anterior and posterior (mesial and distal) faces are roughly equal on M^1, but on M^{2-3} the posterior face is progressively shorter, and on M^4 it is so short that the cross section or coronal outline of that tooth is almost triangular. Lingual faces are simply and gently rounded. Buccal faces are flattened and have very faint vertical grooves or concavities that come to correspond in course of wear with notches between points that develop on the enamel of the buccal wall. As viewed from the buccal side, M^1 develops a low, small anterior and a higher, broader pos-

[12] At this point it is assumed that these animals are marsupials. The evidence is given in the course of the present section on anatomy.

TABLE 2. MEASUREMENTS OF UPPER TEETH OF ARGYROLAGIDAE

	M^1		M^2		M^3		M^4		LM^{1-4}	LM^2/LM^4
	L	W	L	W	L	W	L	W		
Microtragulus reigi										
MMMP No. 691-S	1.5	1.3	1.4	1.4	1.4	1.2	0.8	0.8	5.2	1.75
MMMP No. 661-S	1.6	1.6	1.7	1.6	1.6	1.4	0.9	1.1	5.9	1.78
MMMP No. 395-M	1.7	1.6	ca. 1½	ca. 1½	ca. 1½	ca. 1½	–	–	–	–
Means	1.60	1.50	ca. 1.5	ca. 1.5	ca. 1.5	ca. 1.4	0.85	0.95	5.55	1.76
Argyrolagus scagliai										
MMMP No. 785-S	1.7	1.8	2.2	1.7	2.2	1.8	ca. 2	1.3	7.9	1.1
MMMP No. 802-M	1.8	1.6	1.9	1.7	1.8	1.5	1.5	1.1	7.0	1.20
MMMP No. 281-S	2.0	1.7	–	–	–	–	ca. 1½	1.3	7.6	–
MMMP No. 973-M	2.1	1.7	2.0	1.9	1.7	1.7	1.4	1.4	7.2	1.21
Means	1.90	1.70	2.03	1.77	1.90	1.67	ca. 1.6	1.28	7.42	ca. 1.17

terior point. M^{2-3} have two points closer to each other and separated by a low prominent notch, one point medial on the buccal face and the other, slightly higher, posterior to it. M^4 tends to develop a single, approximately medial point.

As seen in crown view or section, M^1, but not the other molars, has anterobuccal or nominally parastylar (possibly paraconal?) lobe or projection. When little worn (e.g., M^4 of MMMP No. 785-S, *M. reigi*, or M^{1-4} of MMMP No. 691-S, *A. scagliai*), the molar crowns have a shallow, apparently quite simple basin, with a papillate rim, the buccal side considerably elevated above the lingual side. The sharp projection of the buccal side is maintained with wear and bears an interesting resemblance to that of *Caenolestes*. The teeth are thickly enameled on all sides. In some specimens there may be a thin coating of cement, especially on the lingual side, but without examination of thin sections this is not definitely established.

As may be seen in Table 2, M^{2-4} and, to less extent, M^1 tend to be decidedly longer than wide in *A. scagliai*, but M^{1-4} are more nearly equidimensional in *M. reigi*. Except for the noted differences in size and proportions, no marked generic or specific distinctions are observed in the upper dentitions.

The two lower incisors, nearly parallel, are procumbent and strongly curved, convex anteroventrally. The alveoli are separated by bone, but the working apices are appressed. I_1 is distinctly larger than I_2. In section the labial face of I_1 is almost simply and slightly convex. The mesial end is bluntly pointed, and the lingual side is gently concave. The short distal side is also slightly concave. The cross section of I_2 is simpler, the labial face definitely and lingual face slightly convex. The greatest transverse width tends to be somewhat anterior, and in some instances there may be a flattening or very slight concavity posterior to this. In some specimens, e.g., MMMP No. 960-M, *M. reigi*, the incisors are surrounded by enamel, and in others, e.g., MMMP No. 714-S, also *M. reigi*, enamel is present only on the labial faces. This is probably an individual age difference, with the latter condition in older individuals. Wear on these teeth is quite unlike that in rodents. The wear surface on I_1 is almost horizontal, slightly concave longitudinally. On I_2 an almost flat surface slopes mesio-lingual to labio-distally.

The lower diastema is short, about equal to or less than the longitudinal dimension of the alveolus of I_2.

In the following paragraphs, the lower cheek teeth of *Argyrolagus scagliai* are first

described, and distinctions of the other known species are then detailed one by one.

The cross section of nominal P_3 is more or less oval, the longer transverse diameter posterior, but also subtriangular from moderate, separate flattening of the buccal, posterior, and lingual faces.

M_{1-4} of *Argyrolagus scagliai* are strongly bilobed by the presence of a deep, sharp, vertical groove (a flexid in rodent terminology) on each of the buccal and lingual faces. These are directly opposite one another and not offset as is usual in rodents and some other groups. The anterior lobe, undoubtedly derived from an ancestral trigonid, is decidedly longer than the posterior (talonid) on M_{1-4}. On M_1 the anterior lobe is narrower, but anterior and posterior are of about equal width on M_{2-4}. Lengths and widths of the anterior lobes are roughly equal. On M_{1-3} the posterior lobes are about twice as wide as long, but on M_4 these dimensions are nearly equal. The anterior lobes are all somewhat but irregularly quadrate. On all, the most anterior point is anterobuccal. On M_1 this forms a slightly lobate projection, but on M_{2-4} this point is only angulate, the angle slightly less than 90°. On the buccal face of M_1 there is a vertical convexity posterior to the lobule, but on M_{2-4} this face is merely flattened. On all, it has an angulate posterobuccal corner, the angle here greater than 90°. The lingual faces of M_{1-4} also have anterior and posterior angles, both greater than 90°, and between the angles all have shallow vertical grooves or concavities. On M_1 the general direction of this face (in horizontal section) is oblique, posterolingual to anterobuccally. The obliquity is progressively less on M_{2-4} and the face is almost fully anteroposterior on M_4. The posterior lobes on M_{1-3} are transversely elliptical; that of M_4 is almost circular but has a posteromedial projection. On young specimens, P_3-M_4 are nearly or quite surrounded by enamel on all faces. On older specimens, the enamel on the lingual face of P_4 is thin or absent. Enamel persists on the lingual faces of M_{1-4} but becomes thin or absent, perhaps from wear, where those teeth are appressed against their neighbors. Old individuals have what may be a thin layer of cement on the buccal faces of M_{1-4}, but one cannot be certain of this without histological study.

P_3 is absent in the type and only known specimen of *Argyrolagus palmeri*, but its alveolus indicates an elongate-oval or subtriangular tooth, much as in *A. scagliai*, but perhaps relatively longer and narrower. M_{1-3} are definitely more elongate in *A. palmeri;* M_4 is shorter relative to M_3. (See Table 1.) The available figures (Ameghino, 1906, fig. 221; L. Kraglievich, 1931, fig. 2) are not wholly satisfactory as to structural details, but they indicate that on M_1 the trigonid is less triangular in *A. palmeri*, without a distinct anterobuccal projection or buccal concavity on the trigonid, and that on M_4 the talonid is shorter, without a posteromedial projection.

In the only known specimen of *Microtragulus catamarcensis*, P_3 is rounded-triangular, about as in *M. reigi*. M_1 is subtriangular, with an acute anterobuccal apex and a flattened buccal face which is plane or very slightly concave on the trigonid, and a relatively posterior flexid entering to about one-fourth the transverse width of the tooth and marking off a very short talonid equal in width to the widest part of the trigonid. The posterior face is nearly flat, meeting the buccal face at a definite angle of about 90°. It curves into the lingual-anterior face, which is a single curved convex surface from posterolingual to anterobuccal, without any concavity or flexid. M_2 differs in being markedly wider, with the anterobuccal angle less acute. M_3 is intermediate between M_1 and M_2 in width but of about equal length. Anterior and lingual faces are somewhat flattened and meet at a somewhat rounded angle, rather than forming a single curve. There is a slight vertical posterolingual concavity, not definite enough or deep enough to be

called a flexid. There is also a vertical concavity on the posterior face. M_4 is elongate oval or almost teardrop in shape, with a rounded trigonid and a much shorter, narrower, subtriangular talonid set off from the trigonid by shallow, rather obscure vertical grooves. All of the molars are quite distinct from those of *Argyrolagus palmeri* or *scagliai*, and that is the reason for confidently referring them to different genera even though the designation of this second genus as *Microtragulus* is uncertain.

The lower cheek teeth of *Microtragulus reigi* are best represented by the type, MMMP No. 960-M, but two other specimens show no marked differences. P_3, present in the type only, is almost circular in cross section, a slightly curved cylinder. M_1 resembles that of *M. catamarcensis*, but the buccal concavity of the trigonid is more distinct, the posterobuccal lobe (or buccal side of the talonid) projects more, and the posterolingual surface is somewhat flattened but not concave or grooved. On M_2 and M_3 the trigonids are more triangular than in *M. catamarcensis*, and there is a shallow but distinct posterolabial groove or rudimentary flexid on both these teeth, directly internal (labial) to the more developed buccal flexid. M_4 has the same great disparity in size between trigonid and talonid as in *M. catamarcensis*, but the two are more distinctly separated and the trigonid is subtriangular, apex forward, rather than circular. As this tooth is poorly preserved in the only specimen of *M. catamarcensis*, the difference may not have been quite as marked as it seems.

For reasons previously stated, knowledge of the dental characters of ?*Argyrolagus parodii* is unsatisfactory. What is known of M_3 and M_4 in that species is sufficiently discussed in the preceding taxonomic section of this paper.

Mandible. No nearly complete mandible is known, but parts of the horizontal ramus, at least, are known in both genera and all named species except *Microtragulus argentinus*. As for the dentition, description will be based primarily on *Argyrolagus scagliai*, and additional or different features in other species will be noted. In descriptions of mandible, skull, and skeleton, occasional comparison will be made with *Caenolestes*. This is a convenience for clarity of description, and of other known South American marsupials, caenolestids are indeed most nearly similar, although, as will later be shown, there is probably no special relationship.

The horizontal ramus is short and deep, the ventral border strongly convex in outline (as seen laterally), and the alveolar border distinctly but less strongly concave. Depth increases from the anterior end to the level of M_4. The two rami are completely separate, even in old animals, and meet on unfused, nearly plane symphyseal surfaces, oval and elongate anterodorsal-posteroventrally. The posterior end of the symphysis is beneath the posterior end of M_1 or anterior end of M_2 but is not clearly distinct from the free lingual surface of the ramus. In MMMP No. 960-M, *Microtragulus reigi*, apparently a rather young but not juvenile individual, symphyseal contact at the posterior parts of the surfaces seems to have been slight and even incomplete.

In MMMP No. 741-M, *A. scagliai*, there is a single mental foramen between the alveoli of I_1 and I_2 and vertically below P_3. The buccal surface of the ramus posterior to this has scattered smaller foramina or punctations of varying size. The most anterior of these, below M_1, is largest, although it is smaller than the indicated mental foramen. It could be considered as a second mental foramen. The lingual surface of the ramus in this specimen is also punctate on the ventral half or a bit more, posterior to the symphysis. MMMP No. 960-M, *M. reigi*, is similarly punctate and has two distinct mental foramina of nearly equal size beneath P_3 and between P_3 and M_1. Other specimens do not clearly show these characters. Both Ameghino's (1906) and Kraglievich's (1931) figures

of the type of *A. palmeri* indicate no mental foramen, although one must have been present.

Only the root or base of the coronoid process or ascending ramus is preserved in known specimens. It arises from a crest that begins on the buccal face of the horizontal ramus about midway (vertically) between ventral and alveolar borders and beneath the anterior end of M_4. It is quite definite from the beginning in MMMP No. 741-M, *A. scagliai,* somewhat less so in MMMP No. 785-S, same species, and still less in two specimens of *M. reigi* (MMMP Nos. 960-M and 714-S). It is prominent in the type of ?*A. parodii,* although apparently not ending so abruptly anteroventrally. Rusconi (1933) considered this a taxonomic distinction, which is possible, although it seems more probable that it is an individual, sexual, or size difference (or two or all of these). Continuing to rise, this crest becomes a prominent lamina posterobuccal to M_4 and then rises upward in the free coronoid process, broken away in all known specimens and of unknown size and shape but clearly short anteroposteriorly and probably low vertically. Between the lamina and the continuation of the alveolar border posterior to M_4 there is a hollow, and in this in all specimens with this part are indications of a foramen evidently communicating with the dental canal. Although I find no previous mention of it in the literature, it is interesting that what is clearly a homologue of this foramen, although small and somewhat variable, occurs in recent caenolestids.

The angle is preserved in MMMP No. 785-S, *A. scagliai,* and was also present in the now destroyed type of ?*A. parodii,* although not perfectly in either case. It evidently was broad, fully inflected, and excavated or forming a large hollow dorsobuccally. On the opposite (lingual) side of this region is a well-developed flange below the strong, concave masseteric fossa, in which there is a small masseteric foramen.

The condylar process and condyle are also present in MMMP No. 785-S, but breaks between these and the horizontal ramus make their precise relationships uncertain. These relationships were apparently better preserved in the type of ?*A. parodii.* The structure in this region in both (doubtful) genera seems to have been essentially the same and was unique. The condyle is far posterior to the short coronoid process. The surface below and anterior to it is broad, nearly flat on the medial side (above the angle), but excavated and with an everted ventral flange on the lateral side, an arrangement slightly developed in *Caenolestes* and well developed in some diprotodonts, e.g., *Phalanger,* in all of which, however, the posterior projection of the condyle is much less. The articular surface of the condyle is directed dorsally, is irregularly oval in shape but about as broad as long, and is almost flat. These characters are *Caenolestes*-like and quite unlike *Phalanger.* As previously pointed out, Rusconi's belief that the condyle in ?*A. parodii* was below the alveolar level was due to an orientation of the jaw confused by its fragmentary nature in his specimen. In fact, the condyle is distinctly above the alveolar level, but it is lower than in most other marsupials. In this respect the argyrolagids are surprisingly more like Dasyuroidea than recent Caenolestoidea or most Phalangeroidea. However, the level of the condyle is much as in Rusconi's figure (1933, fig. 4) of the extinct caenolestid *Paraepanorthus.*[13] It is not so surprising that the condylar level is similar to that in jerboas, which are convergent to argyrolagids in many respects.

Skull. The following specimens include significant parts of the skull:

Argyrolagus scagliai. MMMP No. 785-S, nearly complete skull. MMMP No.

[13] I consider *Paraepanorthus* as a synonym of *Palaeothentes.* I have not seen a specimen with the condyle preserved and have not checked the possibility of post mortem distortion.

802-M, cranium and region of cheek teeth. MMMP No. 281-S, left premaxilla, zygoma, and adjacent parts of maxilla and ear region.

Microtragulus reigi. MMMP No. 691-S, most of skull. MMMP No. 661-S, most of right maxilla.

As before, description will be based primarily on *Argyrolagus scagliai,* and especially on MMMP No. 785-S, but details will be added from the other specimens listed and differences will be noted.

The habitus of the skull is highly characteristic and very striking, even at first glance. It is extremely different from that of any other known marsupials but has considerable functional resemblances to some placental rodents, especially Dipodomyinae (in the family Heteromyidae) and Dipodidae. These resemblances are clearly convergent among animals not related beyond the subclass level (Theria). They do not extend to details, and there are also major characters that are nonconvergent. Convergence and function will be further discussed in a later section.

The most striking over-all characters are: the long, slender snout protruding far in advance of the incisors; the enormous orbits and broad interorbital region; the posterior position of the orbit and apparent absence of a temporal fossa; the short, globular cranium; the auditory porus opening posteriorly as well as laterally; the large foramen magnum opening rather ventrally; and the enormous palatal vacuities.

The long snout projects well anterior to the incisors. It retains about the same narrow width but becomes shallower anteriorly. The lower part is formed by the premaxillae, which here meet so that the tube is closed, and the upper part is formed by the nasals. Sutures are unfused in what appear to be fully adult individuals. The narial aperture is imperfect in both specimens retaining the snout (MMMP Nos. 281-S and 691-S) but evidently was undivided, anterior, opening somewhat anteroventrally. I know of no other animals with such a structure. As close an approach as any is perhaps that of *Dipodomys,* which has a bony projection anterior to the incisors, but this is relatively short and is formed by the nasals only, being open ventrally. The snout of *Caenolestes* is also elongated, but in an entirely different way: it is the anterior part of the palate that is elongated, and there is no projection beyond the incisors. The anterior part of the palate in Argyrolagidae is, indeed, relatively much shorter than in Caenolestidae. The prepalatal projection of the bony snout must, of course, indicate a long, slender nose, but does not indicate a flexible proboscis. *Macroscelides,* which has such a proboscis, has no prepalatal bony projection, and *Dipodomys,* which has such a projection (although short), has no proboscis. It is interesting that another fossil South American marsupial, *Necrolestes,*[14] also has a peculiar pre-incisor prolongation of the bony snout. In other respects, however, this feature is so different in the two groups that it can hardly be considered as convergent and clearly is not homologous.

The premaxillo-maxillary suture rises vertically from the alveolar margin for almost the whole depth of the face, and at the dorsal extreme of the premaxilla there is a short, sharply pointed posterior projection between the maxilla and the nasal. The incisive foramina are large, short, and broad relative to those of *Caenolestes,* in keeping with the fact that this region of the palate is relatively much shorter and somewhat broader. The premaxillo-maxillary sutures on the palate are not entirely clear but seem to have been about as in *Caenolestes* or indeed most marsupials, with the premaxilla forming the anterolateral part of the rim of each foramen, rather more of that rim than in *Caenolestes,* and the premaxillae together forming most

[14] This genus was long considered an insectivore and has also been referred to the Edentata, but Patterson (1958) has produced convincing evidence that it is a marsupial. See his paper, and its references, for description.

of the medial bar between the foramina with a shorter maxillary extension forming the posterior part.

Posterior to the incisive foramina, there is a short transverse bar formed by the maxillae, and this is followed from the level of the anterior end of P^3 to the posterior edge of the palate, posterior to M^4, by enormous posterior palatal vacuities. These extend laterally to the alveolar margin, so that there is no bony palate at all medial to the cheek teeth. On the specimens including this region there is no medial bar between the posterior vacuities, as preserved, but this may have occurred and been broken away. If so, it must have been very slender. The posterior border of the palate is also broken in all specimens, but there are indications that it was a slender transverse bar, doubtless formed by the palatine bone although the maxillo-palatine suture is not clear, with a palatal ridge, lateral nodular processes, and a posterolateral foramen on each side, as in *Caenolestes* and many other marsupials.

The fenestration of the bony palate is great, even for a marsupial. The fenestration is also extensive in Recent caenolestids, but less than in argyrolagids. Some other South American marsupials, including some caenolestoids and all borhyaenoids, exhibit an opposite trend, with the fenestration reduced or even lost entirely (see Sinclair, 1906; Paula Couto, 1952).

The maxillo-frontal suture is not perfectly clear in any of the specimens, but in MMMP No. 802-M, it seems to run obliquely anteromedial-posterolaterally from the contact of the maxilla with the posterior expansion of the nasals to the anterior part of the dorsal rim of the orbit. On the facial part of the maxilla, a single small infraorbital foramen occurs almost halfway, vertically, from the alveolar rim to the dorsal surface of the face above the anterior edge of P^3. This point is about halfway from the anterior rim of the orbit to the tip of the snout, despite the fact that the snout is so exceptionally long.

It is a concomitant of the strange orbital structure, absolutely unique, as far as I know, and further described below, that although the infraorbital foramen is thus unusually anterior to the orbital aperture, the bony canal leading to it is very short, indeed practically absent. This is best seen in MMMP No. 661-S, *M. reigi*, which is a maxilla broken in such a way as to show both external and internal relationships of the infraorbital foramen. The foramen is between the long intra-alveolar part of P^3, which curves anterodorsally, and that of M^1, which is nearly vertical and divergent from that of P^3. (These parts of M^{1-4} are nearly parallel and close to each other.) The foramen does not lead to a canal but opens directly into the large space open in the bony skull, because of the palatal vacuities, and above the soft palate in life. Hence there are signs of a groove, indicating the probable presence of a non-bony conduit, running posteriorly along the medial face of the alveolar part of the maxilla. Other specimens, especially MMMP Nos. 281-S and 785-S (both *A. scagliai*), strongly suggest but do not quite conclusively demonstrate that this conduit left the orbital cavity through a foramen approximately dorsal to the posterior end of the palate, hence considerably posterior to the anterior part of the orbital space and to the usual position in marsupials or most other Theria. This peculiarity is consonant with the fact, to be considered below, that in argyrolagids the anterior part of the orbital space did not contain the eyeball and with the suggestion that it may have contained a slip of the masseter musculature.

The facial surface of the maxilla anterior to the infraorbital foramen is gently hollowed. The anterior root of the zygoma, formed by the maxilla, is lateral to M^{1-2}. It has a small but distinct ventral process. The maxillo-jugal suture cannot be surely identified, perhaps because of cracks in this area or perhaps because it is in fact closed, as often occurs in marsupials even

while many other sutures are still open. I also fail to detect the lacrimal or its foramen. It is possible, but only just possible, that it is at the anterior part of the dorsal rim of the orbit, as it is in *Dipodomys* and some other rodents but not in any marsupial known to me, other than these argyrolagids.

The posterior ends of the nasals are approximately above M^2 or M^3. They are slightly expanded and have simply rounded sutures against frontals.

The orbit is among the most peculiar features of these altogether peculiar creatures. It is extremely large, and its orifice is directed mainly laterally but also somewhat dorsally and posteriorly. Anterior to the orifice, the cavity of the orbit extends forward for a distance almost two thirds that of the anteroposterior length of the orifice, but this extension is not visible laterally or dorsally. Dorsally it is roofed by a plate formed mainly by the frontal and maxilla but possibly including the lacrimal. Laterally it is covered by a plate probably composed mostly by the maxilla but probably also including the anterior end of the jugal and possibly the lacrimal. The surfaces here spoken of as plates have no evident separation and are essentially a single, curving surface, although the most dorsal part is essentially horizontal and the most ventral part essentially vertical, facing not simply laterally, but also anteriorly and slightly ventrally. In MMMP No. 785-S there are openings in each side of the dorsal surface of this plate, but these are probably artifacts and cannot be confirmed on the other specimens, none quite perfect in this region. The bottom of the anterior part of the orbital space, between the posterior part of the maxilla and the anterior end of the zygoma, is open.

Posterior to the anterior orbital roof, its edge continues as a sharp rim on the dorsal and posterior borders of the orbit. A similar rim continues from the anterior border of the orbital orifice along the dorsal part of the zygoma and then curves around the lateral and posterior sides of the dorsal surface of the glenoid (or articular) process. At the posteroventral part of the orbit there is, in the two specimens of *A. scagliai* that have this region, a slight gap or lowering of the rim, and in the specimen of *M. reigi* with this region the rim is here definitely interrupted for a short space. With the stated exception, the rim of the orbit cuts off the whole space enclosed in the zygomatic arch from dorsal or lateral parts of the parietals and squamosals, which have smooth surfaces without sagittal, temporal, nuchal, or other crests.

This strange orbital and circumorbital anatomy raises serious questions as to masticatory muscles and functions. As close a structural analogue as I can find is again in *Dipodomys*, in which the orbit also extends anteriorly in a pocket covered by bone dorsally and dorsolaterally, somewhat as in the argyrolagids but less extensive. In *Dipodomys* the temporal musculature is greatly reduced. This must also have been true of the argyrolagids, which evidently had a miniscule single slip of temporal muscle originating on the squamosal above the meatus or possibly as far posteriorly as the mastoid. This correlates with the fact that the coronoid process of the mandible was certainly short (anteroposteriorly) in argyrolagids, as in *Dipodomys*, and probably also low, also as in *Dipodomys*. In *Dipodomys*, however, the weakness of the temporal muscle is balanced by a powerful masseteric complex, and the covering of the dorsoanterior part of the orbit is correlated with the origin of a large masseter major anterior to it. (For the osteology and myology of *Dipodomys* see especially Howell, 1932.) Such a muscle cannot have occurred in the argyrolagids. They doubtless had a masseter originating on the zygomatic arch and its anteroventral process, and perhaps another slip from the lateral face of the rostrum. It is logically probable that part of the masseteric muscular complex arose actually within the orbit in its anterodorsal pocket. This seems the

more likely as the origin of the masseter profundus of *Dipodomys* and some other rodents is, if not exactly the same, at least similar. The possible analogue of the masseter profundus in argyrolagids had not invaded the infraorbital canal as in the so-called hystricomorph rodents.

Much of the bizarre appearance of the argyrolagid skull is due to the unique structure and placing of the orbit. The anterior part of the orbital space, which is covered dorsally and laterally and cannot have contained a functional eye, is in the position of the orbit in "normal" mammals, or indeed "normal" vertebrates in general. The posterior part of the orbital space, which clearly contained the eye,[15] is in the position of the temporal fossa. A functional temporal fossa, virtually universal in other mammals (and their ancestors and reptilian relatives), is here practically absent.

The broad frontals, not fused at the midline in the specimens including them, are smooth, slightly convex from side to side, somewhat domed posteriorly. The sutures against the parietals are transverse, slightly convex posteriorly. The frontals form at least the central part of the dorsal rim of the orbital aperture. Posterior and posteroventral to this the situation is not clear in the available materials, but it is probable that the parietals do not quite reach the apertural rim and that another element intervenes in the posterodorsal part of the rim. This could be the squamosal or the alisphenoid. The posteroventral part of the rim is formed by the squamosal, as are the glenoid process and posterior root of the zygoma. The glenoid surface is almost perfectly flat and is oval, with the slightly longer axis anterolateral-posteromedial. From it the squamosal extends forward, as a tapering, jointed process forming the dorsal part of the zygoma, to the anteroventral part of the orbital rim. The jugal has a similar pointed process forming the ventral part of the arch, directed posteriorly and reaching the anterolateral part of the glenoid surface.

The parietals are smooth, broadly domed, and pass posteriorly into the supraoccipital without an intervening crest or ridge but with a decided change in curvature. The rounded occiput, directed for the most part posteroventrally, has a limited, almost equidimensional area for nuchal musculature above the relatively large foramen magnum and between the mastoids. The foramen magnum, transversely elliptical, is directed rather more ventrally than posteriorly, and its lower half is bordered by the narrow condyles, which almost, but not quite, meet ventrally. With the skull oriented on the alveolar or palatal plane, the condyles are directed almost straight ventrally. The head must have been carried approximately at right angles to the neck, which agrees with skeletal evidence that these animals were fully bipedal.

There is a large exposure of the mastoid between the auditory porus and the occiput. This is inflated, but on closer study rather less than might appear on first sight —the globular brain case gives an impression of inflation not really involving very large epitympanic sinuses such as occur in *Dipodomys*, for example. The whole region posterior to the orbitotemporal fossa is much shorter and narrower than in *Dipodomys* and is, in fact, quite like that of *Caenolestes*, despite some adaptive differences related to size, posture, and moderately increased inflation of the middle ear.

The porus acusticus is rather large and is directed posterolaterally and not at all ventrally, an unusual character. There is a tympanic ring, apposed but not fused to the bulla, not developed into a meatus, and closely similar to the tympanic of *Caeno-*

[15] The hypothesis that this is, in fact, a temporal fossa and that a functional eye was reduced or lacking cannot be seriously entertained. In spite of its position this space has all the features related to a large eyeball and its muscles, and the relationship to the brain and cranial foramina is also appropriate. Moreover, these were certainly very active, saltatory animals that could not possibly have had reduced vision or none.

lestes except for the orientation of the aperture. On MMMP No. 785-S there is a small foramen above the porus. This may be homologous with the foramen identified as postglenoid in *Caenolestes* by Dederer (1909), if homology can be deduced from relationship to the ear rather than to the glenoid process. In *Caenolestes* the posterior root of the zygoma is above the porus, the glenoid surface is immediately lateral to the bulla, and the foramen in question is literally postglenoid. In *Argyrolagus* the root of the zygoma is anterior to the porus, and the glenoid is still farther anterior. The foramen is, indeed, posterior to the glenoid but so far away and so unrelated to it that "postglenoid" seems an inappropriate description or identification.

There is a closed alisphenoid bulla, considerably larger and more inflated than in *Caenolestes* or most other marsupials, ovoid with the axis directed posterolatero-anteromedially. This is relatively larger in the smaller *M. reigi* (MMMP No. 691-S) than in *A. scagliai* (MMMP No. 785-S).

The basicranium is partly preserved in the two specimens just mentioned, but most of the details are obscure in both. There appear to be carotid foramina and a transverse canal in the basisphenoid, much as in *Caenolestes* and many other marsupials. From the anteromedial point of the bulla on each side there is a short, small, longitudinal crest ending in a spicular process pointing anteriorly. Dorsolateral to these and immediately anterior to the bullae are two foramina, presumably the foramen rotundum and sphenorbital foramen. These are relatively much more posterior than in *Caenolestes*, or most other mammals for that matter. Their position is correlative with the extreme posterior position of the functional orbits and virtual absence of a temporal fossa. I cannot clearly make out other cranial foramina.

Skeleton. The following postcranial skeletal materials definitely referable to this family are available. Field data are here given for specimens not included in specific hypodigms in the taxonomic section.

MMMP No. 785-S, associated with skull and jaws previously described, and part of the type of *Argyrolagus scagliai.* Atlas and eleven caudal vertebrae; sacrum and pelvis; fragment of scapula; parts of both humeri and of one radius and one ulna; both femora; both tibiae and fibulae (fused); five tarsals; metatarsals of both sides; three pedal phalanges.

MMMP No. 638-M. Humerus, lacking proximal end. Collected in May, 1956, by V. D. Martino in the coastal cliff between Arroyo Seco and Punta San Andrés. Probably Barranca de los Lobos Formation.

MMMP No. 693-M. Nearly complete humerus and distal end of another, perhaps same individual. In the same vial is another fragment of a humerus, not the same individual and probably not this family. From the upper level of the San Andrés Formation, 500 meters south of Punta San Andrés.

MMMP No. 795-S. Nearly complete humerus. Collected by O. Reig, 8 April 1952, south of the Arroyo Lobería. Bed II of the Vorohué Formation.

MMMP No. 395-M. A large lot of bones, mostly minor fragments. Parts of jaws in this lot are referable to *M. reigi*, and the lot has been listed in that hypodigm. The other fragments represent several individuals (at least three and probably more), some perhaps not of this family. The most useful specimens are three complete humeri, three nearly complete femora, and a calcaneum, representing probably two individuals of the same species.

MMMP No. 691-S. In addition to the skull of *M. reigi*, listed in the hypodigm and described above, this number includes a broken tibio-fibula labeled "Asociado al cráneo [de] Microtragulus." "Asociado" means that it was found with the skull but not necessarily that it belongs to the same individual. It is rather improbable that the skull and tibio-fibula, and nothing else, of one individual would be buried together.

However, it is highly probable that the tibio-fibula is of the same species as the skull, *M. reigi.*

MACN No. 4743. This number has been written, evidently at a later date, on Ameghino's label "Microtragulus argentinus" which accompanies the metatarsals that were his essential type for that species. The metatarsals are now in a separate small vial placed in a larger vial that bears the number 12925. In the larger vial are three articulated tarsals, which are probably the basis for Ameghino's reference to cuboid, scaphoid, and cuneiforms in his original description of *M. argentinus* (see taxonomic section, above). There are also fragments of five vertebrae, probably proximal caudals, not mentioned by Ameghino, and several nondescript scraps. It is not clear why these materials in the vial numbered 12925 are separated from the metatarsals, which must belong with the label numbered 4743, but the tarsals, at least, must be part of Ameghino's type or hypodigm of *M. argentinus.*

The skeleton will be described in this sequence: vertebrae, anterior girdle and limb, posterior girdle and limb. MMMP No. 785-S includes the atlas, sacrum, and eleven caudal vertebrae associated with the skull and jaws, type of *A. scagliai.* The atlas is in general stouter than in *Caenolestes* (for which, throughout this section, see Osgood, 1921), as befits a larger and, in all probability, more active animal. The arch is simple, but its mediodorsal part is expanded anteroposteriorly so that in dorsal aspect it appears not as a simple transverse band but as a strongly elongated ellipse or lozenge with rounded corners. The neural canal is not a simple ellipse but has the form of two widely connected ellipses, a larger above and a smaller below. This is suggested but is less pronounced in *Caenolestes.* The short transverse process has a relatively large vertebrarterial canal. Breaks on both sides have laid this open, but it was almost certainly a closed canal or, being short, a foramen in life. This is not present in specimens of caenolestids known to me. Osgood (op. cit.) shows a "nutrient foramen" in this position, but that is so small that it probably could not contain a vertebral artery and is unlikely to be a homologue of the large opening in *Argyrolagus.* The neural canal is closed below by a relatively slender transverse bar with a short ventral process, much as in *Caenolestes.* The condylar articular surfaces are more complex in form than might be anticipated from the condyles themselves, as shown better in the illustration than by words. Above each there is a groove on the cranial side of the neural arch. The articular facets for the axis are fairly simple, widely separated ovals, about as in *Caenolestes.* A possible facet for the odontoid process is vague.

The sacrum consists of two ankylosed vertebrae, as usual in marsupials. Both the broad transverse process of the first sacral and the slender process of the second articulate fully with the ilium. There is a large vacuity between the processes of the two vertebrae. The prezygapophyses of the first sacral and postzygapophyses of the second are well developed, but those between the two are completely fused and form merely a vague prominence. A low medial crest represents poorly developed fused neural spines. The centra are compressed dorsoventrally. The neural canal continues through the sacrum, but is here quite small.

With this same specimen are four anterior caudal vertebrae, which articulate well enough with the sacrum and then with each other and so are probably the first four caudals. The prezygapophyses, present on all of them, are slender processes directed anterolaterally. They become progressively shorter on successive vertebrae. Shorter and narrower postzygapophyses are present on the first and second vertebrae and possibly on the third (here somewhat broken) but are absent on the fourth. All these four vertebrae have well-developed transverse processes, broken on

the first two caudals but probably also progressively shorter (transversely). The stout centra are dorsoventrally compressed. The presumed first caudal has a complete and relatively large neural canal, and this continues through the second, although narrowing rapidly. There are traces of it under the short neural arches of the third and fourth vertebrae preserved, but it is here so small as to be doubtfully functional. The first vertebra has a distinct, although broken, neural spine, but the next three have only a slight longitudinal ridge in this position. These four vertebrae considerably resemble what Osgood numbers as the second to fifth caudals in *Caenolestes* but are somewhat shorter, have more elongated prezygapophyses, and have traces, at least, of the neural spine. What Osgood calls the first caudal is fully fused, both medially and at the ends of the transverse processes, with the preceding unquestionably sacral vertebra. Its transverse processes do not quite touch the ilia in dried, noncartilage skeletons, but it might well be considered sacral or, at least, pseudosacral rather than flatly caudal. In any case, no third vertebra was fused with the sacrum in *Argyrolagus*.

The five poorly preserved vertebrae mentioned above as probably associated with the type of *Microtragulus argentinus* also are probably anterior caudals. If so, that species, at least, had not less than five caudals generally similar to the four just described for *Argyrolagus scagliai*. They are smaller than those of *A. scagliai* in about the same proportion that the metatarsals are smaller. They also have broader, more flattened neural arches and less protruding zygapophyses.

With MMMP No. 785-S, *A. scagliai*, are seven more posterior caudals, possibly but not certainly successive among themselves and to the four described above; thus they are perhaps caudals five to eleven, and, are certainly not more anterior than those. As in *Caenolestes*, they are abruptly unlike the more anterior caudals. The stout centra are much more elongated, there are no neural canal, transverse processes, or zygapophyses. On the first one or perhaps two there are vestiges, only, of a neural arch. All the vertebrae have paired, nubbinlike dorsal and ventral processes at the anterior end and paired, somewhat alar, lateral expansions at the posterior end. The apparently most posterior of these vertebrae is almost as long as any of the others and only moderately more slender. As would be expected in a bipedal, saltatory animal, *Argyrolagus* clearly had a long, heavy tail, much as in kangaroo rats and jerboas. However, *Caenolestes* and some other quadrupeds also have long, stout tails.

The scapula is known only by a scrap of its distal end, part of the same specimen, type of *A. scagliai*. There is nothing particularly distinctive about this. The spine in its distal part seems relatively anterior, but as the prespinous part of the blade probably expanded above this, the spine may have been about medial over-all, as in *Caenolestes*. The acromion is broken away, and its shape or extent cannot be judged. The distal part of the posterior part of the blade has a somewhat thickened rim. The articular fossa is an anteroposteriorly elongate oval. The base of the coracoid process is rather stout, but the process itself is broken away.

The same specimen includes most of the left humerus, lacking the proximal end, and the distal half of the right humerus. There is a well-developed deltoid ridge, somewhat shorter (proximodistally) but somewhat more expanded than in *Caenolestes*. There is a large entepicondylar foramen, as in *Caenolestes*, but differing in that there is a projecting crest anterior to its medial opening, so that opening is not visible in anterior view, both openings, however, are visible in a slightly posteromedial view. The supinator ridge differs markedly from that of *Caenolestes*, being much more prominent and more elongated proximodistally. On the right humerus of this specimen, where it seems to be un-

broken, its lateral edge does not flair beyond the ectocondyle but it is almost straight proximodistal. The distal articulations of these specimens do not differ markedly from those of *Caenolestes*. In both humeri there is a supratrochlear aperture that seems to be a natural foramen.

MMMP No. 638-M, a humerus also lacking the proximal end, is similar to those just described, even to having a probable supratrochlear foramen. All the other humeri listed above also have apertures in this position, although that of MMMP No. 396-M is very small. In no case can artifacts be absolutely ruled out, but this repetition makes it extremely probable that a natural foramen here characterizes the group.

In the lot catalogued as MMMP No. 395-M there are three nearly complete humeri. Two, although not exactly alike, are possibly from one individual. The other is obviously from a different individual and is somewhat larger. In all the supinator ridge flairs strongly externally above and lateral to the ectepicondyle, thus differing from MMMP No. 785-S, which certainly is *A. scagliai*, and 638-M, which probably is. The width across the distal articulation (trochlea plus capitellum) is relatively and absolutely less in 395-M. The argyrolagid teeth in this lot are of *Microtragulus reigi*, and the femora, significantly smaller than those known for *A. scagliai* (see below), almost certainly are also. It therefore seems probable that these humeri belong to *M. reigi*. This is supported to some, but not a conclusive, degree by the facts that only *M. reigi* has been positively identified from teeth in the formation from which they come (Barranca de los Lobos), and that if these humeri do not belong to *M. reigi*, none of those known do. These are somewhat smaller than humeri referred to *A. scagliai*, but the teeth, skull, and femora referred to *M. reigi* are still smaller than those of *A. scagliai*. There is thus a reasonable probability that *M. reigi* had relatively larger front legs than did *A. scagliai*. These humeri preserve the proximal ends, which are not particularly distinctive and closely resemble those of *Caenolestes*, including the fact that the so-called lesser tuberosity is higher and more prominent than the so-called greater tuberosity.

The other known humeri, MMMP Nos. 396-M and 795-S, do not add to morphological knowledge and are of uncertain affinities, being to some extent intermediate between those referred to *A. scagliai* and *M. reigi*.

The right ulna is completely preserved in MMMP No. 785-S. It is generally quite similar to that of *Caenolestes* but somewhat stouter, relatively deeper anteroposteriorly. The olecranon is about equally long. The distal end is stout and has a distinct but short styloid process. The proximal end of the right radius of the same specimen is preserved. It was entirely free of the ulna, as was the distal end, as shown by the ulna. Its head is circular and it has a definite, strong tuberosity. No tuberosity is seen on the ulna, but it is slightly damaged in this region.

No bones of the manus are known.

Except for the blade of the left ilium, the pelvis is almost completely preserved in MMMP No. 785-S. It is radically unlike the pelvis of *Caenolestes*. Many, although not all, of the differences are resemblances to saltatorial rodents and hence may be considered locomotory adaptations adding to the many other convergent characters among argyrolagids and, especially, kangaroo mice and jerboas.

Howell (1932) has pointed out some supposed trends in transition from quadrupedal to extreme bipedal saltatory locomotion in rodents. Although Howell's conclusions seem to be invalid or, at best, unsubstantiated,[16] the homologous figures

[16] Measurements on Howell's fig. 15 differ radically from the figures given on p. 519, and my figures for *Dipodomys* also differ greatly from his. He has either taken the measurements in

in Table 3, based on my measurements, are of interest (p. 66). The length of the ischium relative to the ilium is about the same in *Argyrolagus* and *Caenolestes* and is slightly, perhaps not significantly, greater in a specimen of *Dipodomys*. This proportion has no evident relationship to bipedality. On the other hand, the postsacral part of the ilium is much longer, which is also to say that the presacral extension of the iliac blade is relatively much shorter, in *Caenolestes* than in *Dipodomys*. In *Argyrolagus* this difference is still greater, the presacral part being actually longer than the postsacral. This does seem to be a bipedal-saltatory specialization.[17]

The great anterior extension of the ilium is accompanied by the flaring of the upper lateral, strongly concave, gluteal surface. The lower lateral, presumably iliac surface, also concave, is smaller. The ridge between them is prominent, as is the tubercle at its posterior end, near the acetabulum. The strong tuberosity of the ischium is the most posterior point of the pelvis, the posterior border ventral to this down to the symphysis being almost vertical but inclined slightly forward. In striking contrast with *Caenolestes*, the symphysis is long, its anterior end below the acetabulum.

The ascending part of the pubis thus is nearly vertical. It almost certainly was not in contact with a marsupial bone throughout the length of its anteroventral edge, as it is in *Caenolestes*, but whether a marsupial bone with less extensive contact was present cannot be determined. The acetabulum is deep, with heavy, high dorsal and anterior rim, but is not otherwise characteristic. There is a low ileopectineal tubercle. The component bones of the pelvis are all fully fused, at the symphysis as well as elsewhere. The pelvic aperture is rather shallow and wider than deep. This and the fused symphysis accord with marsupial reproduction, with extremely small offspring at parturition. (In *Dipodomys* and many other small placentals the aperture is deeper than wide; the symphysis is unfused and the two sides of the pelvis here separate when parturition of the relatively large young occurs.)

Both femora are present, only slightly damaged, in the type of *A. scagliai*. The femur is closely similar to that of *Caenolestes;* the most striking distinction is not structural but is that the femur of *Caenolestes* is shorter than the humerus, whereas in *Argyrolagus* it is more than twice as long as the humerus. The head is approximately spherical and almost sessile, with a short, barely constricted neck. The greater trochanter extends proximally distinctly above the head of the right femur but not quite up to the level of the head on the left femur. Both have been affected by crushing, and the original condition was probably intermediate. The digital fossa is long and slitlike, almost exactly as in *Caenolestes*. The intertrochanteric ridge is present but forms a somewhat rugose mass rather than a crest, and its extremity is distinctly separate from the lesser trochanter, which is flaring and proximal. A smaller third trochanter is distal to the greater trochanter, opposite the lesser trochanter but with its apex slightly more distal. The long shaft, almost circular in section, has a graceful sigmoid curve, slightly concave anteriorly in the proximal part and convex in the medial and distal parts. The distal end has a broad, shallow patellar groove, strongly suggesting but not proving the existence of a bony patella.

The three femora under MMMP No. 395-M are not quite so well preserved. They are closely similar to those just described but are decidedly smaller and somewhat more slender. The neck may be

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some different way or has entered them incorrectly at some point in his research. Moreover, further on p. 519 his figures show an increase in distance from acetabulum to sacral articulation with increasing bipedalism, but in the next sentence he says that the distance has been shortened.

[17] As Howell (1932) concluded, although his numerical values seem to show the opposite. Howell did not find a satisfactory functional explanation.

more constricted, the intertrochanteric ridge less definite, and all the proximal features less strongly developed, but these may be effects of faulty preservation. These bones almost certainly belong to *M. reigi*. As previously noted, they are somewhat smaller relative to the humeri believed to be of that species (or the humeri are somewhat larger relative to them) than in *A. scagliai*.

The tibia and fibula, known in MMMP No. 785-S, are fused proximally just at the point of contact and with a visible line of separation. Distally, from about the middle of the shafts onward, they are completely fused, with no visible line of separation. A greater or less degree of fusion occurs in kangaroo rats, jerboas, hares, and some other leaping placentals but not in caenolestids. The proportions and general characters are, however, otherwise rather *Caenolestes*-like. The proximal half, approximately, of the tibia is triangular in section, with a greatly produced cnemial crest reaching its greatest eminence about one-sixth of the way down the shaft and thereafter gradually fading out. The anteromedial face is gently convex, the anterolateral hollowed out and more strongly concave. The much shorter posterior face, somewhat bowed forward, is gently convex from side to side, with a slight medial longitudinal ridge in its upper part. The whole tibia in this proximal portion is bowed anteromedially away from the fibula, which is almost straight. The distal part of the shaft of fused tibia and fibula is polyhedral in section, with six angulations of varying prominence. The tibial part of the distal end has the usual articulation for the astragalus and a well-developed internal malleolus. The fibular part, projecting beyond the astragalar articulation, has a well-developed facet that articulates with the calcaneum.

MMMP No. 691-S includes a tibiofibula lacking the distal end and imperfect elsewhere, referred with little doubt to *M. reigi*. The preserved parts compare closely with the latter, but the cnemial crest is even more produced proximally, although it falls away more abruptly and at a less distal point.

An astragalus, both calcanea, a cuboid, an ectocuneiform, and a possible navicular of *A. scagliai* are preserved with MMMP No. 785-S. The body of the astragalus is larger than the head and the broad, very shallow trochlea occupies almost its entire width on the dorsal (or anterior) side. The head is not quite as wide as the body and is very short and sessile, without a distinct neck. On the ventral (or posterior) surface the trochlea ends in a sharp flange overhanging the sustentacular and part of the ectal facets. Those two facets are of nearly equal size, the ectal concave and the sustentacular more nearly plane, almost in contact with each other but at slightly different levels. There is no astragalar foramen. The most decided difference from *Caenolestes* is the less distinct, less projecting head.

The tuber of the calcaneum (or os calcis), unlike that of *Caenolestes*, is stout, decidedly longer than the body of the bone, and expanded posteriorly. The ectal facet, central on the body, is moderately convex, and the sustentacular facet, not clearly separated from the ectal and at a slightly lower (or more posterior) level, is more distinctly convex. Internal and slightly distal to these facets is a third of about equal size, transversely semicylindrical. This articulates with the fibular side of the distal end of the tibiofibula and is either absent or much less definite in *Caenolestes*. A small tubercle disto-external to this is probably homologous with what Osgood (1921, p. 96 and pl. XVI) calls in his text a facet for the tarsometatarsal ligament and in his figure a facet for a ligament to the astragalus of *Caenolestes*. On the dorsal or anterior surface the bone projects beyond the ectal, sustentacular, and fibular facets at a lower, or more posterior, level. The distal, cuboid facet is distinctly double. The external part extends farther distally

and is more convex. Between the two is a short, sharp step, along which contact with the cuboid continues. There is a hint of this rather odd condition in *Caenolestes*, but it is not so distinct.

In correlation with the peculiar cuboid facet of the calcaneum, the proximal surface of the cuboid has two facets and a step between them, the external facet more distal. The distal surface of the cuboid articulates strongly with metatarsal IV and lightly with the process on it interpreted below as the fused proximal end of metatarsal V. The cuboid probably associated with the type of *Microtragulus argentinus* is closely similar but smaller, as are all known parts of that species.

There is doubt about the navicular. In the partial tarsus probably of *M. argentinus* there is a bone articulated in this position. It articulates with a single bone, presumed to be the ectocuneiform, distally on the anterior or dorsal surface. This distal part projects more posteriorly than the presumed ectocuneiform, and if there were meso- and entocuneiforms they must have been very small and have lain here rather than in the more usual position medial to the ectocuneiform. Above this posterior or plantar part of the mooted navicular, a long and stout styliform process projects proximally. It is possible, but improbable, that this bone has not been articulated correctly and that it is not in fact a navicular or is a wrongly oriented navicular. With MMMP No. 785-S there is a bone of somewhat similar but far from identical shape, which I cannot articulate satisfactorily with other preserved parts. It may or may not be a navicular. In this individual the probable ectocuneiform is articulated with the left metatarsals and there is indeed a small posterior space that could have contained one or two more cuneiforms.

As previously noted, the essential type of *M. argentinus* consists of metartarsals III and IV, and these, both left and right, are also present in the type of *A. scagliai*. These bones in the two species are practically identical in character except that those of *A. scagliai* are decidedly longer and slightly stouter. Contrary to Ameghino's belief, and mine on first sight, metatarsals III and IV of *M. argentinus* are not fused and therefore do not form a true cannon bone. They are very closely appressed, with flat, slightly irregular contacting surfaces, and they adhered to each other through fossilization, as did several of the nevertheless separate tarsals. Separate motion of the two metatarsals or motion of one relative to the other must have been quite limited or nil. The metatarsals of MMMP No. 785-S, *Argyrolagus scagliai*, have also adhered to each other, and I have not ventured to try separating them. However, it seems highly probable that, as in *M. argentinus*, they are appressed but not fused. These bones also have the peculiarity that the two, together, are slightly skewed. If the proximal parts of the two bones, in normal contact, are placed on a flat surface, a line across the distal ends is not parallel to that surface, but the end of metatarsal IV is above it, or is relatively more anterior or dorsal than the end of III.

Those distal ends are slightly divergent and are of the same length, that is, are equally distal. Their phalangeal articulations are globular anteriorly, transversely cylindrical posteriorly, there each with a median keel. Proximally the metatarsal believed to be IV projects slightly farther than the other. It articulates with the bone interpreted above as the cuboid. In this individual a tarsal, interpreted as the ectocuneiform, is preserved in articulation with the left metatarsals. Its distal articulation is with the more medial metatarsal, believed to be III, only. On this specimen there is a separate slip of bone extending down onto the posteromedial surface of metatarsal III but there quickly wedging out. Proximally it is stouter but extends almost as far as the cuneiform. The other metatarsal III of this individual and the type of *M. argentinus* have articular facets

for this bone. It could be a mesocuneiform, but it seems more probable that it is a much reduced metatarsal. In either case, there was no digit on this side of the bone identified as metatarsal III. On the side of the proximal end of metatarsal IV there is a short styloid process, distal to which there is a posteromedial swelling of the bone quickly dying out in the distal direction. There are slight concavities between this and the body of metatarsal IV but no distinct line of fusion. Ameghino (1904) interpreted this (in *M. argentinus*) as the fully fused, functionless, proximal end of another metatarsal. This is probable, although not certain. In any event, no facet for apposition of another separate metatarsal is visible here. The conclusion is almost forced, although perhaps not absolutely certain, that these animals had only two toes on the pes, without even vestiges of others beyond the proximal ends of the metatarsals.

The homologies of the two fully developed metatarsals are of importance both functionally and phylogenetically. Believing *Microtragulus argentinus* to be a ruminant artiodactyl, Ameghino (1904) naturally considered the supposed cannon bone to be formed by metatarsals III and IV, and as far as I know all later students have accepted that without further discussion. However, if *Argyrolagus* were a diprotodont or phalangeroid, as L. Kraglievich believed and Rusconi agrees, that homology would be virtually impossible. In all phalangeroids, metatarsals II and III are reduced and the corresponding digits are syndactylous and always somewhat, usually much, shorter than IV, often also shorter than V. As further treated in discussion of relationships, such feet are basic for diprotodonts and probably antedated the origin of that group as such. If *Argyrolagus* had that ancestry, its supposed cannon bone (the two large, appressed metatarsals) would practically have to be IV and V. However, in that case these two bones together would articulate largely or wholly with the cuboid proximally. In fact, each of the two articulates wholly with a quite separate tarsal. There can be little doubt that these are the cuboid and ectocuneiform, that the tarsals are, indeed, III and IV, and that Ameghino was right (for the wrong reason). Such a foot could readily evolve from a more generalized one as in *Caenolestes*,[18] but not from a perameloid or phalangeroid foot.

MMMP No. 785-S included two proximal and one distal phalanges. The proximal phalanx is arched dorsally (or anteriorly). The concave proximal articulation is at an angle of about 45° with the long axis of the bone, suggesting that the toe was normally carried at an angle of about 135° with the metatarsal. This articulation is notched proximoventrally, corresponding with the metatarsal keel. On the plantar side there are convex nubbins on each side of the notch. The distal articulation is simply convex in a longitudinal direction and straight in transverse section. It is mostly on the plantar side of the bone. The distal phalanx is a sharp, only slightly recurved claw, strongly compressed from side to side. The articulation is a semilunar notch directed proximoplantarly. Anterior to it on the plantar side is an elongated projecting process, swollen at proximal and distal ends. This terminal phalanx seems small and weak in proportion to the proximal phalanx and other limb bones, but the probability is great that it does belong to the same individual.

AFFINITIES

Former views. Ameghino (1904) based *Microtragulus argentinus* on two supposedly fused metatarsals, or a "cannon bone," mentioning also other metatarsals, cuboid, scaphoid (=navicular), and cuneiforms, without description further than

[18] In his generally excellent monograph on *Caenolestes* Osgood (1921, pp. 96–97 and plate XVI) has misidentified the cuneiforms, and his statement of their relationships to the metatarsals is impossible.

saying (in Spanish) that they were "constructed, like the other bones, on the same type as the Tragulidae." Apart from reference to the Tragulidae, no further discussion of relationships was given pending "a special notice accompanied by figures" (in Spanish). That notice was never published, but in his final polemic stratigraphic volume (Ameghino, 1906, p. 344) a figure (fig. 177) of the metatarsals, only, was given along with the following remark:

"What I never suspected was that the selenodont artiodactyls might also be of South American origin. That origin is indicated by the recent discovery at Monte Hermoso of part of the skeleton of a tiny artiodactyl that has been given the name of *Microtragulus argentinus*."[19]

This seems clearly to indicate that Ameghino then considered *Microtragulus* as ancestral or prototypal for selenodont artiodactyls. That was, however, anomalous even from Ameghino's own point of view. He considered *Microtragulus* as late Miocene in age, and selenodont artiodactyls that he considered older, Oligocene at least, were already well known from North America and Europe. He later (Ameghino, 1912) still considered *Microtragulus* as "the smallest and most primitive known selenodont artiodactyl" (original in French), yet not as ancestral to all other selenodonts, and as African, not South American nor yet North American, in origin. The geographic aspect of that is considered elsewhere in this study. The point here is that Ameghino continued to consider *Microtragulus* as a primitive selenodont artiodactyl.

As far as I have been able to discover, that opinion was never accepted by anyone else. L. Kraglievich said in passing that *Microtragulus* might be a rodent or a diprotodont marsupial (1932), and he later (1934) listed it as a rodent. Castellanos (1934) said, also in passing, that it is not an artiodactyl but a rodent. Those opinions seem to be the only ones expressed after Ameghino and before the close relationship of *Microtragulus* and *Argyrolagus* was recognized.

The type lower jaw of *Argyrolagus palmeri* was discovered in the same beds, those of Monte Hermoso, at approximately the same time, early 1904, and by the same collector as the type of *Microtragulus argentinus*. The earliest opinion as to the affinities of *Argyrolagus*, although not published until much later, was expressed by the collector, Carlos Ameghino, in a letter to his brother Florentino dated from Monte Hermoso on 11 May 1904:

"Of rare genera, besides the ursid already mentioned, there finally has come to light a plagiaulacid, which I had a sort of yen to discover. It is a very small lower jaw, as small as *Epanorthus minutus*, but very peculiar. Its aspect is surprising, the molars apparently with open roots, somewhat like those of *Pithanotomys*, and it seems quite likely to me that this is that extremely rare genus known as *Tribodon clemens*. The dental formula comprises four true molars and a small styliform premolar, and the incisor is as in the paucituberculates of Santa Cruz. I believe it is a descendant of *Promysops* of the *Notostylops* beds."[20]

[19] "Ce que je n'avais jamais soupçonné c'est que les artiodactyles sélénodontes pouvaient être aussi d'origine sud-américaine. Cette origine est indiqué par la découverte faite récemment à Monte-Hermoso, d'une partie de squelette d'un tout petit Artiodactyle qui a reçu le nom de *Microtragulus argentinus*. . . ."

[20] "De géneros raros, además del Ursídeo ya mencionado, ha aparecido, al fin, un Plagiaulacídeo, que tenía como antojo de encontrar. Es una mandíbula inferior muy pequeña, tanto como *Epanorthus minutus*, pero muy singular. Es de un aspecto sorprendente, con los molares al parecer de base abierta, algo parecidos a (los de) [probably an insertion by the editor] *Pytanotomys* [sic!] y me parece muy probable que se trate de aquel género rarísimo conocido por *Tribodon clemens*. La fórmula dentaria se compone de 4 verdaderos molares y de un pequeño premolar anterior estiliforme y el incisivo es como en los Paucituberculados de Santa Cruz. Yo creo que es un descendiente de los Promysop [sic!] del Notostilopense."

The plagiaulacids, strictly speaking, are late Jurassic and early Cretaceous multituberculates. In the Ameghinian system, however, the term referred loosely to an assemblage including also Polydolopidae and Caenolestidae and believed to extend, in part ancestrally, to the Australian diprotodont marsupials and the placental rodents and lagomorphs. (Ameghino did not consider marsupials and placentals as distinct taxonomic groups.) *Epanorthus* is a caenolestid, but Carlos Ameghino refers to it only for comparison of size, not as a matter of affinity. *Pithanotomys* and *Tribodon* are both (true placental) rodents from Monte Hermoso. Don Carlos not only indicates this as a true relationship but also considers it likely that this specimen belongs to a species of *Tribodon*. *Promysops* (= *Eudolops*) is a polydolopid marsupial. The Ameghinos considered this genus ancestral to placental rodents and lagomorphs. Don Carlos's opinion that this specimen is a descendant of *Promysops* thus does not contradict his belief that it might belong to *Tribodon*, a genus of rodents.

In referring to this letter, then unpublished but evidently read by him, Rusconi (1933) said that Don Carlos had considered this mandible as "somewhat related to the marsupials of Patagonia." He later (Rusconi, 1967, p. 283) said that Carlos Ameghino, in the letter here cited, had identified *Argyrolagus* as a marsupial of the group of the Paucituberculata (= Caenolestoidea). He then contrasted Don Carlos's field identification, believed to be at least approximately correct, with the incorrect cabinet identification by "Dr. Florentino." In fact, Don Carlos did not identify *Argyrolagus* as a marsupial or a paucituberculate. He clearly stated his belief that it was a rodent and even indicated possible pertinence to a previously named genus of rodents. The only suggested connection with marsupials depended on the Ameghinos' belief (now of course known to be unfounded) that all rodents (and lagomorphs) were derived from forms that we now classify as marsupials.

When he first published on this specimen, Florentino Ameghino (1904) agreed with Don Carlos in considering *Argyrolagus*, then named, a rodent *sensu lato*, but rather as a duplicidentate, that is, a lagomorph, than a simplicidentate.

"The representatives of this new family . . . from the original stock for the Lagomorpha or duplicidentates and are the most primitive known rodents. The discovery of this family solves the hitherto mysterious origin of the duplicidentates, showing that they arose from the Promysopidae independently of the other rodents."[21]

As noted previously, *Promysops* is in fact a polydolopid and is synonymous with a genus, *Eudolops*, that Ameghino himself referred to the Polydolopidae. However, that does not matter much as regards Ameghino's views on *Argyrolagus*, since he believed that the "Promysopidae," and hence through them both lagomorphs and rodents, were earlier derived from the Polydolopidae. It does matter that Ameghino considered *Argyrolagus* implicitly as ancestral to and explicitly as more primitive than the lagomorphs, although he believed it to be late Miocene in age and knew of North American Oligocene lagomorphs. He later (Ameghino, 1906) made it clear that he considered the Agyrolagidae ancestral to the lagomorphs through (unknown) earlier members of the family and not through the late genus *Argyrolagus* itself. He then figured the type specimen of *Argyrolagus palmeri* (Ameghino, 1906, p. 368, fig. 221).

Like *Microtragulus*, *Argyrolagus* was long ignored by most other students of South American mammals, or of mammals

[21] "Los representantes de esta nueva familia constituyen el tronco de origen de los *Lagomorpha* o duplicidentados y son los roedores más primitivos que se conocen. El descubrimiento de esta familia viene a resolver el origen de los duplicidentados que era hasta ahora un misterio, demonstrando que se han separado de los *Promysopidae* independientemente de los demás roedores."

in general. For example, it figured neither in Scott (1913) nor Schlosser (1923). However, L. Kraglievich (1931) later refigured and redescribed Ameghino's type and added another species, *A. catamarcensis* from the Araucanian beds. He noted correctly that the structure is quite different from any lagomorphs, but resembles diprotodont marsupials, by which he meant the Australian group I (e.g., Simpson, 1945) call Phalangeroidea, excluding the Caenolestoidea (Paucituberculata of Ameghino and Kraglievich). The only resemblances definitely stated were: the shapes of the inflected angle and masseteric flange, compared with those of *Trichosurus;* the presence of a masseteric foramen, correctly stated to be present in some but not all phalangerids; and the number and form of the incisors and molars, said to show affinities with phalangerids but not more explicity compared. He also said that there are slight resemblances (one must so understand "ligeras afinidades") with the Paucituberculata (Caenolestoidea), but that *Argyrolagus* differs much more from them than from the phalangerids. However, no difference from the caenolestoids was specified. In fact, the angle and masseteric flange are quite like those of recent caenolestids, and these also have a masseteric foramen more like that of *Argyrolagus* than is that of *Trichosurus.* The lower dental formula of *Argyrolagus* is in fact like that of *Trichosurus* and other relatively primitive phalangerids: 2.0.1.4. However, the upper formula (unknown to Kraglievich) is not; 3.1.2.4 is primitive for phalangerids, but the formula is 2.0.1.4 in *Argyrolagus.* The whole *Argyrolagus* formula could just as well be derived from the primitive caenolestid formula, $\frac{4.1.3.4}{3.1.3.4}$, and the form of the teeth of *Argyrolagus,* especially the incisors, differs greatly and about equally from both recent phalangeroids and recent caenolestoids, none of which have two enlarged, rodentlike incisors in the lower (and still less in the upper) jaw.

Thus Kraglievich did not in fact give any valid reason for referring *Argyrolagus* to the Phalangeroidea or for excluding it from Caenolestoidea. He further and correctly excluded "Promysopidae" (= Polydolopidae) and Polydolopidae from ancestry to this genus, but his statement that the ancestry therefore did not occur in Patagonia is a non-sequitur, and in any case absence from Patagonia would not argue against caenolestoid or for phalangeroid affinities. Kraglievich was, however, on safe grounds in recognizing the Argyrolagidae as a distinct family, whatever its affinities may be.

Shortly after publication of Kraglievich's paper, Rusconi (1933) described still another presumptive species, *A. parodii,* from the Chapadmalalan. He then adopted Kraglievich's views as to affinities, saying (in English) that "there is no probability of the existence of a link between [the Polydolopidae and Caenolestidae] and the *Argyrolagus* group," and deriving the "argyrolags" from "primordial phalangerids." He supposed the low position of the condyle of *Argyrolagus* to be archaic but the dentition to be highly specialized and supposed that "the ancestry of the argyrolags can be traced successfully in this manner." Neither of these characters is phalangeroid, and no evidence of such affinities was given except citation of Kraglievich. "The paucituberculated marsupials of Patagonia," that is, fossil caenolestoids, are said to "represent a group of mammals that evolved in a different way from *Argyrolagus.*"

In the meantime, before Rusconi's paper was published, I (Simpson, 1932) pointed out the improbability and inadequate evidence of special affinity between *Argyrolagus* and Australian diprotodonts and hazarded a guess that it might be an aberrant typothere. That guess was extremely wide of the mark, although my principal point of non-community of origin with the phalangeroids can still be sustained.

When Rusconi wrote his paper of 1933, he had not seen mine of the previous year. He later (1936) firmly rejected reference to the Typotheria and insisted on marsupial affinities. He was quite right on both counts. In that same paper Rusconi (1936, p. 181 or p. 11 of the separate) said, "My *a priori* impression is that the cannon bone of *Microtragulus argentinus* would seem to belong in the hind limb of *Argyrolagus*, an idea with which Don Carlos Ameghino, its discoverer, also agrees."[22]

In discussion of affinities in that paper, Rusconi was primarily concerned with proof that *Argyrolagus* is not a typothere. He gave a list of thirteen non-typothere characters and said that five of these are typical of many marsupials: last molar bilobed, second lobe small; strong perpendicular masseteric crest below last molar; large masseteric fossa with a masseteric foramen; strong, inflected angular process; probable dental formula $\overline{1.0.1.4}$. Not all of these non-typothere characters are diagnostically marsupial, but the case is made. In addition, Rusconi called attention to the canal behind the last molar and noted that it occurs in some paucituberculates (caenolestoids) in the Tertiary of Patagonia. (It also occurs in recent caenolestids.) No more evidence of phalangeroid affinities was given, and no definite statement of the place of the argyrolagids in the Marsupialia, although there is an implication that they are not considered caenolestoids.

In view of all that discussion and of his frequent distrust of Ameghino's work, it is peculiar to find Scott in 1937 (p. 240) no longer ignoring *Argyrolagus* but assuming that Ameghino was right in calling it a lagomorph, indeed a rabbit.

Since Rusconi's paper of 1936, synonymy of *Argyrolagus* and *Microtragulus* and reference to the Marsupialia have been accepted by a few writers, but there has been no further first-hand published research and little mention of this group. For example the family is not mentioned in the almost exhaustive French Traités of zoology and of paleontology. Following Rusconi's paper of 1936, I (Simpson, 1945) provisionally accepted reference of *Argyrolagus* to the Marsupialia. In 1955 Reig (1955, p. 61) formally indicated synomymy of *Argyrolagus* with the prior name *Microtragulus*, named the family Microtragulidae, and referred it to the Caenolestoidea. That was done on the basis of specimens, then unpublished, described in the present study (Reig, 1955, footnote on p. 60). Reig later (1958, p. 249) again indicated the generic synonymy and listed the Microtragulidae among the Marsupialia.

Romer (1966, p. 379) has listed the "?Microtragulidae" with "*Microtragulus* [*Argyrolagus*]" in the Polyprotodonta, which he distinguished both from the Caenolestoidea and from the Diprotodonta. Affinities are not discussed, but the hierarchical and sequential arrangements imply separate origin from the Didelphidae.

Most recently Rusconi (1967, p. 284) has again noted that *Argyrolagus* and *Microtragulus* (which is consistently misprinted "*Microtagulus*" and in Spanish vernacular "Microtagulo") may be synonymous, but he is rather less positive than in his 1936 paper and he fails to note that in case of synonymy it is the name *Argyrolagus* that is invalidated. He continues to consider these animals as related to the Australian diprotodonts (misprinted "diprodontes" in the Spanish text) rather than to any other South American marsupials. He now definitely refers the Argyrolagidae to the otherwise Australian superfamily Phalangeroidea. (He erroneously also includes

[22] "Mi impressión, a priori, es que el *os canon* de *Microtragulus argentinus* parecería corresponder al miembro posterior de *Argyrolagus*, ideas [sic, plural] a la cual se adhiere también Don Carlos Ameghino, su descubridor."

It is not clear to me in what way this idea is to be considered as *a priori*.

The agreement by Carlos Ameghino was presumably in personal communication. Don Carlos, long chronically ill, died in the year of the publication in question.

New Zealand in the distribution of the superfamily.) No new evidence for this view is given.

Present views. The argyrolagids are now fairly well known, thanks to the specimens described in this account, and there is a relatively good basis for determining their affinities. Nevertheless they are so peculiar that their status remains somewhat dubious even now.

These animals are unquestionably marsupials. No single one of their known characters would be typologically diagnostic (none is present in all marsupials and no placentals), but the following combination of characters is conclusive:

Four molariform teeth and less than four premolars.

Large palatal vacuities.

Alisphenoid bullae.

Probable transverse canal and entocarotid foramina in basisphenoid.

Angular process of mandible strongly inflected.

Masseteric foramen present.

Long, fused pubic symphysis and shallow pelvic outlet.

The presence or absence of a marsupial (epipubic) bone, highly characteristic of marsupials but not present in all of them, has not been determined. If present, its contact with the pelvis was slight and non-sutural, but that is common in (other) marsupials.

The present question, then, is not whether the argyrolagids are marsupials—they certainly are—but where they belong among the varied ranks of marsupials. Here the first point, obvious throughout the preceding descriptions and the illustrations, is that argyrolagids have many peculiarities that are rare, less developed, or completely absent in any other known marsupials. The most striking of these are:

Presence of two, somewhat rodentlike, rootless incisors in each side of each jaw, upper and lower.

Five continuously growing cheek teeth on each side, above and below.

Very long snout, projecting as a closed bony tube anterior to the upper incisors and palate; palate short.

Large anterior orbital space covered by bone dorsally and laterally.

Eyeball in extreme posterior position.

No distinct temporal fossa.

Globular cranium with some hypo- and hypertympanic inflation.

Metatarsals III and IV appressed, extremely elongated.

Only two functional toes in pes.

Other pecularities represent functional specializations that occur in more or less similar form, evidently by convergence, in a number of different groups, both marsupial and placental. Most obvious of these are the characters associated with bipedal saltation, such as the small fore legs, enlargement and distal elongation of hind legs, and long, heavy tail.

These and other less striking but also peculiar characters show that the argyrolagids are an extremely aberrant, highly specialized group. Surely no one could question their reference to a distinct family, as proposed by Ameghino from the start and accepted without reservation in every subsequent reference to the group (as represented by *Argyrolagus*). The questions then are (a) at what hierarchic level, family or higher, the argyrolagids should be separated from other marsupials, and (b) with what other taxon, if any, below the level of subclass or infraclass Metatheria the argyrolagids may be naturally[23] associated.

[23] By "naturally" I of course mean evolutionarily or phylogenetically. Phenetic classification, sometimes wrongly called "numerical," if pursued without any evolutionary concepts, would almost certainly classify argyrolagids not as marsupials at all but as rodents rather closely related to Dipodidae, Heteromyidae, or both. I believe that this is a case in which the most extremely exclusive pheneticists will find the combination of phenetic evidence with evolutionary interpretation more natural, in some sense, than a strictly

Consideration of affinities within the Metatheria involves some decision as to recognition of other natural subordinate taxa within that taxon. It is still true that the largest taxa, or rather those of highest category within the Metatheria, generally accepted as natural evolutionary groups are approximately those I listed in my now old classification (Simpson, 1945) as superfamilies. With the emendations noted, these are:

Didelphoidea (I now include the Borhyaenidae, which clearly arose from didelphids and most of which are not radically divergent.)
Dasyuroidea
Caenolestoidea
Perameloidea
Phalangeroidea

There are aberrant or little-known forms of doubtful status that might eventually also merit superfamily distinction, for example, *Necrolestes* (now in the Didelphoidea), *Notoryctes* (in the Dasyuroidea), *Groeberia* (in the Caenolestoidea), or *Vombatus* and *Tarsipes* (in the Phalangeroidea), but as minimal major groups the five named seem surely to be natural, and the marginal forms that may represent additional major groups do not matter for present purposes. None has any special resemblance to the argyrolagids, with the possible exception of *Groeberia* and *Vombatus*, mentioned below.

These taxa, variously named and ranked, have often been grouped at higher categorical levels, suborders or orders, within the Metatheria. Classical arrangements, a more recent proposal by Ride (1964), and a new suggestion are as follows:

(As Suborders)		(Suborders)	
Polydactyla	Didelphoidea Dasyuroidea Caenolestoidea	Polyprotodonta	Didelphoidea Dasyuroidea Perameloidea
Syndactyla	Perameloidea Phalangeroidea	Diprotodonta	Caenolestoidea Phalangeroidea

Ride, 1964 (As Orders)		Alternative suggestion (Suborders)	
Marsupicarnivora	Didelphoidea[24] Dasyuroidea[24]	Herpetotheria	Didelphoidea Caenolestoidea
Paucituberculata	Caenolestoidea[24]	Eometatheria[25]	Dasyuroidea Perameloidea Phalangeroidea
Perameline	Perameloidea[24]		
Diprotodonta	Phalangeroidea[24]		

Of these arrangements, I somewhat prefer Ride's. Still another arrangement, taking account of Ride's but different in some important respects, has been based on additional, especially serological evidence by J. A. W. Kirsch. It may be still more acceptable, but it has not yet been published and cannot be discussed here. All of these groupings are decidedly moot, there is no established consensus, and for present purposes, at least, I prefer to discuss affinities in terms of the superfamilies specified above, without reference to suborders or multiple orders.

In these terms, the Perameloidea can be ruled out as possible ancestors or significantly close relatives of the Argyrolagidae. An ancestor of the Perameloidea that could also be an ancestor of the Argyrolagidae would almost certainly be a primitive dasyuroid and not taxonomically a perameloid. Argyrolagids could have evolved from very primitive, probably Cretaceous, didelphoids or dasyuroids, simply because any

mechanical (or supposedly "objective") phenetic interpretation. I do not mean by this remark to deny either the validity of strictly phenetic classification entirely on its own grounds, understood to be devoid of any evolutionary significance, or its great usefulness as evidence and adjunct for evolutionary classification and for functional interpretation (not classification). I only want to point out a striking example in which most biologists will generally prefer the latter alternatives.

[24] Ride does not recognize these groups as such, eschewing the superfamily level and dividing Marsupicarnivora into six, Paucituberculata into three, and Diprotodonta into five families.

[25] Reference is to the east, not to the dawn.

or all marsupials could be derived from such primitive sources. Argyrolagids are so different from such a source and so extremely specialized with respect to it that they would have to be placed in a separate superfamily (at least), if that is the extent of their relationship to other marsupials. (I return to this and suggest that such is indeed the case on a later page.) The Argyrolagidae are obviously very unlike any late, or for that matter any known Caenolestoidea or Phalangeroidea. However, that does not rule out, *prima facie*, derivation from early Caenolestoidea, after that group had differentiated from Didelphoidea (or Dasyuroidea), or from early Phalangeroidea, after that group had differentiated from Dasyuroidea (or Didelphoidea). Acceptance of one or the other of those views would indicate reference of the Argyrolagidae on one hand to the Caenolestoidea or Paucituberculata, on the other to the Phalangeroidea or Diprotodonta.

A first point in considering these various possibilities is the resemblance of argyrolagids to the Vombatidae.[26] That taxon, aberrant in the Phalangeroidea but usually referred there, includes the only known marsupials other than argyrolagids with continuously growing teeth. The wombats further resemble argyrolagids in having fewer than three upper incisors, no canines, and five cheek teeth. P^3_3 are subtriangular and M_{1-4} are bilobed, further as in argyrolagids. However, special resemblances end there. The incisors are different both in number, $\frac{1}{1}$ $\left(\frac{2}{2}\right.$ in argyrolagids$\left.\right)$ and in functional aspects (more definitely rodentlike in vombatids), and the upper molars are deeply divided on the labial side (not there divided at all in argyrolagids). The snout is unusually short and does not project anteriorly to the incisors. The orbit is relatively small and anterior. There is a particularly large temporal fossa and a small, not at all globular cranium. The animals are heavily quadrupedal, ambulatory, virtually tailless, and fossorial. Special affinity of argyrolagids and vombatids seems impossible. Any relationship could be, at most, by derivation of both from basic phalangeroids (or diprotodonts), and the limited dental resemblances must have evolved separately in the two groups.

Relationship with the Phalangeroidea must next be considered, especially because the only two students who have previously published extensive studies of argyrolagids, L. Kraglievich and Rusconi, agreed in referring them to that group (as Diprotodonta, with caenolestoids excluded). It must be remembered that their knowledge was limited to incomplete lower jaws and that present disagreement is based on much more extensive evidence than was available to them. (My own interpretation of the lower jaws then available was far wider of the mark than theirs.) In the preceding review of previous views on affinities, it was shown that the few characters specified by L. Kraglievich or Rusconi as evidence of phalangeroid affinities are either also present (in some instances more nearly similiar) in caenolestoids, or of even wider occurrence, or contradicted by later knowledge. That is still true of the lower jaws and their dentitions: they have no characters suggestive of phalangeroid, as distinct both from caenolestoid and from merely general marsupial, affinities.

Present knowledge of the skulls of argyrolagids, not involved in previous publication, confirms and strengthens that situation. The upper dentition has no resemblance to phalangeroids except for those few to Vombatidae (and not to any other or to primitive phalangeroids) mentioned above and evidently not homologous.

[26] "Phascolomidae" in Simpson (1945) and many other studies. That may also be the legal name under the current code. However, it is now fairly well established that the name of the type genus should be taken as *Vombatus* rather than *Phascolomis*.

The lower and upper incisors could be described as literally diprotodont, but as regards the upper incisors, at least, this is a difference from, not a resemblance to, the so-called diprotodont marsupials. The argyrolagid snout resembles those of perameloids and some caenolestoids to a limited extent in being elongate and more or less tubular, but is thereby entirely unlike any phalangeroid. The ear region, with an epitympanic sinus, complete and somewhat inflated bulla, but no extended meatus, is quite different from that usual or probably primitive for phalangeroids. No special character *sui generis*, among the many in the argyrolagid skulls, is hinted at in any known phalangeroid.

The hind foot is also decidedly *sui generis* in argyrolagids, in a way relevant to phalangeroid affinities and practically conclusive against them. In the preceding anatomical section it was shown that the functional metatarsals are almost certainly III and IV and that all others are absent or reduced to functionless vestiges without appended phalanges. As is well known, in all phalangeroids (and perameloids) digits II and III are syndactylous, that is, each is slender, they are enclosed proximally in a common integument, and they function essentially as a single toe. That cannot have been true of argyrolagids. The longest digit in phalangeroids is IV. II and III, together, and V may be of approximately equal length and almost as long as IV, as in most Phalangeridae and probably primitive for Phalangeroidea. In some more advanced phalangeroids, notably the Macropodidae, II-III and V both tend to be reduced, and the foot may become almost (although never quite in living or known fossil forms) monodactylous on IV. In some forms, e.g. *Dendrolagus*, II-III is reduced but V is large (not quite so large as IV), and there is a tendency toward didactyly on IV and V. Didactyly on III and IV has not and really could not have evolved in this group.

It appears that the hind foot of argyrolagids could not have arisen from a syndactylous ancestry. On the other hand, in the didactylous groups Didelphoidea, Dasyuroidea, and Caenolestoidea, pedal digits III and IV are commonly subequal, larger than II and V, and quite separate from the latter. The condition in argyrolagids, although far advanced beyond that, could readily have arisen from it.

All recent or known fossil phalangeroids are both syndactylous and diprotodont. It has been a moot question which condition evolved first and which might therefore be taken as a key character in the original differentiation of the taxon. Those are of course the alternatives involved in classifying marsupials in two suborders, Didactyla and Syndactyla if syndactyly was believed to antedate diprotodonty, but Polyprotodonta and Diprotodonta if diprotodonty was supposed to antedate syndactyly. But the Perameloidea are syndactylous and polyprotodont, whereas the Caenolestoidea are didactylous and diprotodont. One should therefore logically conclude either that syndactyly evolved independently in Perameloidea and Phalangeroidea or that diprotodonty evolved independently in Caenolestoidea and Phalangeroidea. Or both might be true. Early authors, Thomas (1895) for one of many examples, tended to consider diprotodonty primary, although they were not always clear that this strongly suggested two separate origins of syndactyly. Only a few recent students still maintain that arrangement. Others have argued that syndactyly arose but once, and that diprotodonty, to the extent that it can be considered similar in both groups, arose independently in Caenolestoidea and Phalangeroidea. That was, for instance, the strong conviction of Wood Jones (e.g., 1923), who included in the argument the statement that, "No didactylous diprotodont marsupial is known," hence implying that the Caenolestoidea, so long and so often considered Diprotodonta, are not diprotodont at all, even descriptively.

Syndactyly is a very peculiar, anatomically and presumably also genetically complex structure and functional arrangement that is not known ever to have occurred in any marsupials other than Perameloidea and Phalangeroidea and that is practically identical in those two. Diprotodonty, defined as enlargement and procumbency of one pair of lower incisors, is a relatively simple development that has occurred independently in many groups of mammals, from the multituberculates already in the Jurassic through numerous quite distinct Cenozoic placentals. The arrangement is not alike in detail in caenolestoids and phalangeroids. There are, of course, many other characters and considerations to be weighed, but it does seem quite probable that syndactyly is monophyletic in marsupials and that diprotodonty is not. The issue is evaded by my arrangement into marsupial superfamilies and also by Ride's into metatherian orders, but Ride's general morphological and phylogenetic diagrams (especially 1964, figs. 1 and 2) clearly show syndactyly as monophyletic and diprotodonty (he calls it "pseudodiprotodonty" in his Paucituberculata = Caenolestoidea) as polyphyletic. I agree.

That bears on the present problem in two different ways. First, it indicates that the ancestors of the Phalangeroidea, even before that group existed as such and had differentiated from the Perameloidea, were syndactylous. The argyrolagids could not have had syndactylous ancestors; therefore they were not derived from phalangeroids and cannot be referred to or placed as next relations to them. This is safer than most single-character phylogenetic inferences, and it is supported by the absence of any contrary evidence among the many and complex argyrolagid characteristics now known.

The second bearing is that the apparently independent origin of diprotodonty (or of diprotodonty and "pseudodiprotodonty") in at least two quite distinct groups of marsupials lessens the evidential value of the distantly similar development in argyrolagids. That is all the more true in that the resemblance of the incisors between caenolestoids and phalangeroids is much greater than that between the incisors of argyrolagids and those of either one of those groups.

In fact, the dentition of argyrolagids is so peculiarly specialized, so radically unlike that of any other known marsupials, that it gives no evidence for relationships below the level of Metatheria. The only particular resemblance to Caenolestidae is the enlargement of lower incisors, but these are different in number and form in the two groups and the upper incisors are entirely dissimilar. Among other caenolestoids, the most primitive known polydolopid, *Epidolops ameghinoi* (see Paula Couto, 1952), does have two pairs of strongly procumbent lower incisors, but they are morphologically and functionally unlike those of argyrolagids, and in *Epidolops* the cheek teeth are already well advanced in a line of specialization completely different from that of argyrolagids.

Comparisons with *Caenolestes*[27] have been made throughout the anatomical part of this study. Numerous fossil caenolestids are known, but from such incomplete materials as to add little or nothing to possible comparisons. Moreover, most of them, notably the Palaeothentinae and Abderitinae of Sinclair (1906), are decidedly more specialized than the surviving caenolestids in the known parts, and specialized in such ways as to be even less similar to argyrolagids. Noted resem-

[27] There are three supposed genera of living caenolestids: *Caenolestes*, with five claimed species; *Lestoros* (usually called *Orolestes*, a preoccupied name), with one; and *Rhyncholestes*, also with one. I suspect that placing of the "genera" as three species would be a better biological arrangement, but evaluation of the slight taxonomic distinctions is not relevant for present purposes. I have made first-hand comparisons with *Caenolestes* and "*Lestoros*." "*Rhyncholestes*" is evidently neither more nor less comparable.

blances of argyrolagids to caenolestids include:

Presence of a foramen and canal posterior to M_4.

Presence of a diminutive masseteric foramen.

Generally similar angular and masseteric regions on mandible.

Flattened, horizontal articular surface on mandibular condyle.

Large anterior palatal foramina and large palatal vacuities.

General, globular shape of posterior part of cranium.

Tympanic similar in shape and in relationship to bulla.

Sharp distinction of anterior and posterior caudal vertebrae and similar structures of both.

Proximal end of humerus and entepicondylar foramen similar.

Generally similar femur.

The number of similarities in such a list, which could be lengthened, is superficially impressive, but only superficially. All of the resemblances are rather general, and most of them are in minor, variable, or evolutionarily plastic details. Many are not exclusive to the argyrolagid-caenolestid comparison but occur in a scattered way among other marsupials (e.g., masseteric foramen) or mammals in general (e.g., entepicondylar foramen). Most of them are aspects of functional systems that are otherwise radically unlike those of caenolestids (e.g., the rather similar femora of the two groups articulate with extremely different pelves, and the distal hind leg segments are also extremely different).

The possibility that argyrolagids evolved from ancestral caenolestoids can hardly be ruled out flatly. If, however, that was their origin, the argyrolagids have diverged to an unrecognizable extent, and no character really diagnostic of caenolestoids is evident in them. When lower jaws and dentitions alone were known, basic separation of argyrolagids from caenolestoids would not have been justified, but the unusually extensive knowledge now at hand not only justifies but, in my opinion, demands such separation.

Two very poorly known taxa of South American marsupials require passing notice at this point: Necrolestidae and Groeberiidae. *Necrolestes*, previously usually placed in the Insectivora and sometimes in the Edentata, was finally shown to be a marsupial (Patterson, 1958). It shares with argyrolagids an elongation of the bony snout anterior to the incisors. In all other characters, however, it is extremely different: number and shape of incisors, presence of large, laniary canines, triangular molars, absence of palatal vacuities, absence of a bulla, and generally fossorial habitus, to name a few such characters. Any special relationship to argyrolagids is impossible.

Groeberia minoprioi, (sole known member of the Groeberiidae) is known only by an incomplete lower jaw.[28] In the original description, Patterson (1952) pointed out some possible resemblances to *Argyrolagus*: enlarged, hypselodont lower incisor with limited enamel and with intraalveolar part parallel with the median line of the symphysis; subequal molars of similar structure; strong, projecting coronoid process; and absence of masseteric crest. However, Patterson also pointed out that there are differences: the dentition of *Argyrolagus* is less reduced and it is much later in geologic time; the molariform teeth are hypselodont; and the symphysis is unfused and normal in structure. Present greatly increased knowledge of argyrolagids shows that the differences, even in the few characters known in *Groeberia*, are even greater than appeared. Although a buccal subcoronoid crest is present in argyrolagids, the coronoid itself is feebler than in *Groeberia* and probably quite different. A well-developed masseteric crest

[28] I have heard of another specimen, but this has not been described and I cannot confirm its existence.

is present in argyrolagids. Patterson was certainly right in concluding that the two groups clearly represent different lines of descent, and there is at present no evidence that they are more nearly related than by being both marsupials. In the present state of knowledge the question is not so much whether the Argyrolagidae are related to the Groeberiidae as whether the latter are especially related to the former, and much the most probable answer is "No."

By the virtual elimination of reasonable alternatives, what remains is the likelihood that the ancestry of the Argyrolagidae separated from other marsupial taxa at a fully basic level in the Marsupialia, among members of the didelphoid or didelphoid-dasyuroid complex. No known member of that complex shows any special resemblance to argyrolagids, and all one can say is that its most primitive members are sufficiently unspecialized that nothing would seem to exclude them from possible ancestry to argyrolagids—or to any other marsupials. As we know only the terminal argyrolagids, there is the possibility that early forms would indicate some more particular links with other marsupials. However, our knowledge of these terminal forms is now excellent, and it does seem to warrant the definite, although negative, step of separating argyrolagids from all other marsupials. In the system I still prefer, that indicates recognition of a superfamily Argyrolagoidea, which at present requires or warrants no definition apart from that of its unique family.

If Ride's (1964) system of dividing the Metatheria into orders were adopted—and there is much to be said for it—the reasonable classification of the argyrolagids would be still more difficult. That is one of the reasons why I still prefer, even if on a "temporary" basis for a generation or two, division of the Marsupialia (and Metatheria) into superfamilies rather than orders or suborders. Distinctive as they are and well-known as they now are, I would be loath to give ordinal rank to this little group, at least until some stronger evidence of its ancestry is available. I also hesitate to assign it to any of Ride's proposed orders. I have given reasons for not placing it in the orders Paucituberculata, Peramelina, or Diprotodonta, which are other names and ranks for the Caenolestoidea, Perameloidea, and Phalangeroidea, respectively. Like those three groups, the Argyrolagoidea probably evolved from very early members of Ride's Marsupicarnivora, yet they have changed so radically from primitive "marsupicarnivores" and in a direction so unlike any (other?) later members of that group that reference to it would seem anomalous.

One remaining point would be whether the Argyrolagoidea arose from Didelphoidea or Dasyuroidea. Those groups were barely or perhaps not distinguishable in their most primitive forms. They are distinguished mainly because their descendants evolved separately and became so very dissimilar. I see no morphological evidence for considering argyrolagids as closer to one than to the other. However, it is fairly clear that the South American radiation of marsupials arose from Didelphoidea and the Australian from Dasyuroidea, and the known Argyrolagoidea are exclusively South American. Geographic distribution is also evolutionary, and its evidence favors origin from the Didelphoidea.[29] Although I think no circularity is really involved in that argument, the question might arise. In any case, the Argyrolagoidea do have zoogeographic significance and have long been considered in that light. I now turn to that aspect of their study.

ZOOGEOGRAPHY

Former views. Both *Microtragulus* and *Argyrolagus* early became involved in zoo-

[29] And therefore reference to the Hesperometatheria, if my only half-serious earlier suggestion for ordinal or subordinal classification were adopted.

geographic discussions. Ameghino (1904) gave no zoogeographic inferences in the original publication on *Microtragulus*. In 1906 (p. 344), however, he was explicit and unequivocal that *Microtragulus* indicated the origin of selenodont artiodactyls in South America and spread (in post-Miocene times!) thence to the rest of the world. In 1912 he radically altered that view:

"Among the artiodactyls those that are surely of North American origin are the llamas or camelids and most of the cervids, but some of the latter, such as *Mazama* and certain fossil forms, are of all the more doubtful origin since the smallest and most primitive known selenodont artiodactyl was found at Monte Hermoso. *Microtragulus argentinus* was no larger than a small rat and it cannot be derived from any of the forms that lived in North America. These primitive forms probably reached South America by the Senegal-Guiana bridge."[30]

That conclusion and the genus itself have usually been ignored, but Castellanos (1934) reacted against Ameghino's last opinion as follows:

"The Senegal-Guiana bridge created by Ameghino did not exist, as I have already indicated in other publications. . . . The mammals of African and European type that Ameghino has coming to South America do not have that character and come from North America. Moreover, the incomplete condition of their remains has lent itself to wrong determinations. Those of *Microtragulus* are not remains of an artiodactyl but of a rodent. . . ."[31]

Ameghino (1904) immediately hailed *Argyrolagus* as indicating a South American origin for the lagomorphs. His definitive statement in 1906, after a page-long review of the question, was that, "In consequence, *Argyrolagus* should be considered as the last representative, and the only one so far known, of a family of rodents[32] forming the origin of all the duplicidentate rodents known from all other parts of the earth" (Ameghino, 1906, p. 368).[33] It is here not absolutely explicit that Ameghino considered that ancestral family autochthonous in South America, but there is no real doubt about the implication. That is conclusively borne out by a diagram on the following page (Ameghino, 1906, p. 369), showing the "Rodentia duplicidentata" as arising, at successively remote times, from the "Promysopidae" [= Polydolopidae], Polydolopidae, "Garzoniidae" [=Caenolestidae], and "Microbiotheriidae" [now included in Didelphidae]. As Ameghino believed, and as is still generally accepted, those are all groups autochthonous to South America and unknown from any other region. It is curious that in this family tree, immediately following the discussion of the supposedly crucial place of the Argyrolagidae, the latter family does not appear.

[30] "Parmi les Artiodactyles ceux qui certainement sont d'origine nordaméricaine ce sont les Lamas ou Camelidés et la plupart des Cervidés, mais quelques uns de ces derniers comme *Mazama*, et certaines formes fossiles sont d'origine d'autant plus douteuse qu'on a trouvé a Monte Hermoso l'Artiodactyle sélénodonte le plus petit et le plus primitif qu'on connaisse. Le *Microtragulus argentinus* n'était pas plus grand qu'un petit rat et on ne peut le faire descendre d'aucune des formes qui ont habité l'Amérique du Nord. Il est probable que ces formes primitives aient pénétré dans l'Amérique du Sud par le pont guayano-senegaléen."

[31] "El puente guayano-senegalense creado por Ameghino no ha existido, habiéndolo manifestado ya en otras publicaciones. . . . Los mamíferos de tipo africano y europeo que Ameghino hace venir a Sud América, no presentan ese carácter y proceden de Norte América; por otra parte, el estado incompleto de los restos se han [sic!] prestado a determinaciones inexactas. Los del **Microtragulus** [boldface in the original] no son de un artiodáctilo sino de un roedor. . . ."

[32] Like virtually all zoologists of the time, Ameghino considered the lagomorphs, or Duplicidentata, a suborder of Rodentia.

[33] "Il en résulte qu'*Argyrolagus* doit être considéré comme le dernier réprésentant, et le seul connu jusqu'à présent, d'une famille de Rongeurs qui constitue la souche de tous les Rongeurs duplicidentés qu'on connait de toutes les autres régions de la terre."

In accord with Ameghino's views, it should have been inserted between "Rodentia duplicidentata" and "Promysopidae."

Kraglievich (1931) considered *Argyrolagus* a diprotodont marsupial and argued as follows, in part, about its zoogeographic significance:

"Most probable is its [*Argyrolagus's*] derivation from the primitive phalangeroid[34] stock and its immigration into Argentine territory toward the end of the Miocene, coming from a region whence the other phalangeroids emigrated to Australia and nearby islands." He then argued that no known Patagonian fossil marsupials could be ancestral to *Argyrolagus*, and continued: "With Patagonia thus excluded as center of origin of *Argyrolagus*, and with even greater reason any other area of America, Africa, Europe, and the Australian region itself, seeing that no animal discovered in those areas can be an ancestor of the one from Monte Hermoso [*Argyrolagus palmeri*], we must perforce refer its origin to a *terra incognita*, perhaps the South Pacific continent, where the primordial phalangeroids could have lived before their radiation, part of them going off in the direction of Australia, and the rest of them to our country [Argentina]. But in that case it is obvious that we must admit a connection of said South Pacific continent with central and northwestern Argentina across Chile (excluding Patagonia) during the Miocene, by which way *Argyrolagus* could have immigrated." The latter point is supported by Kraglievich's description of *A. catamarcensis*, considered ancestral to *A. palmeri*, from Catamarca, a considerable distance northwest of Monte Hermoso. Kraglievich concludes: "This extraordinary discovery [of *A. catamarcensis*] strengthens the suspicion of a probable western immigration by *Argyrolagus*, which postulates the elongation toward the west of a large part of the South American continent, far beyond its present limits, around the middle of the Tertiary."[35]

The existence of a South Pacific continent was assumed, and no real reason was given for assigning the origin of phalangeroids, hence also of argyrolagids according to Kraglievich's views, to that hypothetical continent rather than to Australia. The implicit negative argument was hollow, because when Kraglievich wrote, only one surely pre-Pleistocene fossil mammal (*Wynyardia bassiana*) was known from Australia and it was, indeed, a phalangeroid. The exclusion of Patagonia from the presumed migration route rested on slightly better, but still completely negative grounds. I (Simpson, 1932) opposed those zoogeographic views and argued that *Argyrolagus* was probably a native South American, but it was in this connection

[34] In writing "falangérido" and "otros falangéridos" Kraglievich did not mean to refer *Argyrolagus* to the Phalangeridae. Immediately before this passage he made clear that he considered the Argyrolagidae a distinct family although rather closely related to the Phalangeridae. I therefore translate "falangérido" as "phalangeroid," not "phalangerid," in this passage.

[35] "Lo más probable es su derivación a partir del primitivo stock falangérido y su inmigración al territorio argentino hacia fines del mioceno, procedente de una región desde la cual los otros falangériods emigraron hacia Australia e islas adyacentes."

"Excluida así la Patagonia como centro de origen de *Argyrolagus* y con mayor razón cualquier otra comarca de America, Africa, Europa y la misma región australiana, puesto que ningún animal descubierto en ellas puede ser antecesor del de Monte Hermoso, debemos forzozamente relegar su origen a una *terra incognita*, quizá el continente surpacífico, donde pudieron habitar los falangéridos primordiales antes de que irradiaran dirigiéndose rumbo a Australia una parte, y a nuestro país la otra.

"Pero en tal supuesto, es obvio que debemos admitir una conexión de dicho continente con la Argentina centro y nordoccidental a través de Chile (excluyenda la Patagonia) durante el mioceno, por cuya vía pudo inmigrar *Argyrolagus*."

"Este extraordinario descubrimiento robustece la sospecha de una probable inmigración occidental de *Argyrolagus*, que supone la prolongación de una gran parte del continente sudaméricano hacia el oeste, mucho mas allá de sus límites actuales, a mediados del terciario. . . ."

that I made the unfortunate guess that it might be an aberrant typothere.

In his first paper on the subject, Rusconi (1933) briefly reviewed Kraglievich's zoogeographic views and concluded: "The paucituberculated marsupials [Caenolestoidea] of Patagonia represent a group of mammals that evolved in a different way; and, according to present knowledge, there is no probability of the existence of a link between them and the *Argyrolagus* group. Neither is there any valid evidence that these Pliocene marsupials of Argentina might have come from the Australian region. Therefore it would not be strange if Kraglievich's theory was proved true some day" (original publication in English).

Later, Rusconi (1936, p. 180) raised but did not attempt to answer two questions: "Have the argyrolags, along with marsupials in general, their origin in the Australian region or perhaps in a South Pacific *terra incognita,* now submerged, from which marsupials would have spread before the Cretaceous, some toward Australia and others toward South America? Or might the argyrolags have reached Argentina from the west and by way of lands now submerged but without having passed through Patagonia?"[36] These apparent alternatives are not really such. Kraglievich and, following him, Rusconi himself had previously answered both questions affirmatively. In the next paragraph, however, Rusconi may possibly imply that the marsupials, wherever they came from, evolved from earliest times quite separately in Australia and South America, and if that is his meaning it might also imply South American origin of the Argyrolagidae. However he made no such definite statement, and this whole discussion is so vague that I am uncertain as to whether he had formed a clear opinion or, if so, what it was.

Most recently, Rusconi (1967, p. 284) has been somewhat more positive, reverting to essential agreement with L. Kraglievich. He states that *Argyrolagus, Microtagulus* [sic! and here retained as a separate genus although suspected of synonymy], and various Paleocene notoungulates have no known ancestors. He concludes: "Their remote ancestors should sometime be found in those broad lands now buried under thick layers of ice of the Antarctic pole, or else in lands now covered by the South Pacific sea, reckoned so to speak as the *terra incognita.* Surely that is whence will some day be afforded the remains of ancestral lineages, and thereby it will have become possible to make an end of so many interesting arguments arising from the study of ancient life. . . ."[37]

The history of study of the affinities and zoogeography of *Microtragulus* and *Argyrolagus* is an appalling mass of inaccuracy, faulty logic, unfounded opinions, and misidentifications. I can say so without snobbery because I contributed something to the confusion. So did one of the greatest authorities on South American mammals W. B. Scott (1937, p. 240): "Of the very numerous Rodentia of the so-called Araucanian stage, only the rabbit (†*Argyrolagus*) was an immigrant from the north, all the others belonging to autochthonous families."

Present status. Decision that the Argyrolagidae are not Phalangeroidea or derived

[36] "Los argirolagos como los marsupiales en general tienen su origen en la región australiana o bien en una *terra incognita* sur pacífica, hoy submergida, y de la cual habrían irradiado antes del cretáceo marsupiales que se hubieran dirigido: unos hacia Australia y hacia sudamérica otros?, o bien, Los argirolagos habrían llegado a la Argentina por Occidente y por tierras hoy submergidas pero sin haber pasado por la Patagonia?"

[37] "Sus remotos antecesores deben ser hallados alguna vez en aquellas extensas tierras sepultadas actualmente por espesas capas de hielo del Polo Antártico, o bien en tierras actualmente cubiertas por el mar Pacífico del Sud, conceptuada en cierto modo como la 'tierra incognita'. Seguramente es de donde proporcionaran algun día los restos de ramales precursores, y con ello, se habrá podido dar termino a tantas interesantes discusiones que surgen del estudio de la vida pretérita. . . ."

from any separate pre-phalangeroid stock at once removes them from providing any possible evidence for a South American-Australian connection in the Southern Hemisphere, whether directly or through Antarctica or by dispersal from an intermediate *terra incognita.* A detailed review of theories of land connections of South America with Australia, on one side, and Africa, on the other, is not called for in this place, but these may be briefly mentioned.

Marsupials figured largely in the hypothesis of a South American-Australian connection, which long antedated L. Kraglievich's zoogeographic views on argyrolagids and was, indeed, becoming obsolete when he wrote. Some early South American didelphids resemble primitive Australian dasyuroids. Some advanced, not early or primitive, South American borhyaenids resemble the advanced Australian dasyuroid *Thylacinus.* Primitive, not exclusively early but not advanced, South American caenolestoids have characters that could have occurred in hypothetical ancestors of the Australian phalangeroids. It has, however, been cogently argued and is now generally accepted that resemblances in primitive features are in general derived from a didelphoid or didelphoid-dasyuroid complex that was widespread in the northern continents and does not require or suggest a southern connection. Resemblance in more specialized characters is not in any case really detailed or extensive, and is more logically explained by convergence than by homology. For example, it seems beyond serious doubt that the more or less *Thylacinus*-like borhyaenids evolved in South America from didelphids and have no closer connection with *Thylacinus.* (The evidence is summarized, with citations of earlier literature, in Simpson, 1948.)

In suggesting that the argyrolagids indicate a South American-Australian faunal connection L. Kraglievich was thus endorsing a hypothesis long sustained but now generally rejected. He was advancing ostensibly new evidence and not reinforcing the supposed caenolestoid-phalangeroid relationship, because he believed that the argyrolagids, interpreted as Diprotodonta along with the Phalangeridae and some other Australian families, were not related to the Caenolestidae within the Marsupialia. His assumption that the connection was through a South Pacific continent between Australia and South America involved another hypothesis that had once had some technical support but that has now been quite conclusively disproved and was, indeed, generally abandoned even when Kraglievich (and still more later when Rusconi) wrote.

As far as mammals are concerned, supposed connection between South America and Africa has involved especially primates, rodents, and sirenians, with the occasional more marginal mention of a few other groups such as proboscideans and hyracoids. That supposed evidence is not relevant here beyond noting that a strong consensus now holds that no direct connection exists among the known terrestrial mammals. The African Miocene *Palaeothentoides africanus* (Stromer, 1932) was at first believed by its describer to be not only a marsupial but also a caenolestoid and hence of South American affinities, but Butler and Hopwood (1957) showed that it belongs in the exclusively African placental family Macroscelididae. (See also Patterson, 1965.) Castellanos (1934, quoted above) was of course right in negating Ameghino's claim that *Microtragulus* migrated to South America from Senegal. That arose from Ameghino's inevitable misidentification of the isolated bones on which *Microtragulus* was based. Castellanos's disagreement involved an equally great misidentification, but his geographic disclaimer was correct and present indubitable identification of *Microtragulus* as an argyrolagid marsupial puts a complete negative to any hypothesis of affinities with Africa.

The present situation is that no argyrolagoids and no identifiable argyrolagid ancestors more advanced than the didelphoid or didelphoid-dasyuroid complex ancestral to all other marsupials are known from anywhere but Argentina. Didelphoids were abundant in South America by the late Paleocene, and they, as well as some other marsupials, were then already highly diverse (e.g., Paula Couto, 1962, on didelphids; Simpson, 1948, on other early marsupials). Although no identifiable marsupials older than the probable late Paleocene have yet been found in South America,[38] primitive didelphoids, conceivably ancestors of the argyrolagoids, must have been there by the late Cretaceous.

On present evidence, then, the most probable view is that the Argyrolagoidea arose in South America from didelphoid ancestors and are another of the numerous groups both autochthonous and endemic in that continent. The only argument against this, now that diprotodont relationships are ruled out, is one advanced by L. Kraglievich and endorsed by Rusconi. The argyrolagoids, highly characteristic and extremely specialized, suddenly appear in the middle Pliocene, at the earliest, without members or recognizable ancestors in any earlier South American fauna. However, the conclusion that they were therefore immigrants from a *terra incognita* in the Pliocene does not follow. Even in Patagonia, with the richest record, it is extremely improbable that all groups of small mammals present between Paleocene and Pliocene have yet turned up in collections. Moreover, Patagonia has always been marginal in South America, as it is now. There are enormous areas with little or no fossil record where groups of limited ecological or climatic distribution could have been evolving without entering the known fossil record.

Because there is no impelling likelihood that argyrolagoids were absent from Patagonia and because there are vast areas elsewhere in South America where they could have originated and evolved, on present evidence there is certainly no reason to believe that they immigrated from the west and north of Patagonia.

In summary, argyrolagoids probably originated in South America in late Cretaceous or early Tertiary time and remained endemic to that continent. It is possible but not demonstrable that they evolved for the most part in central (now tropical) South America and spread to the more marginal southern zone from which their remains are known in the late Tertiary. It is highly probable, but again not demonstrable, that they evolved under special ecological conditions poorly sampled by the known fossil record.

Finally, in view of recently revived interest in the theories of continental drift and of Gondwanaland, a remark on those may be added. The evidence of the argyrolagoids agrees with and to that extent reinforces the view that South America had no land connection with either Australia or Africa during the late Mesozoic and Cenozoic. It thus adds a small additional item, of no great significance in

[38] Early supposed records of mammals older than late Paleocene were shown long since (Simpson, 1932) either not to be definitely mammalian or not to be of the supposed ages. A subsequent discovery is that of Jurassic tracks believed by Casamiquela (1961) to be mammalian. If mammalian, they are unidentifiable as to subclass or order and cannot be compared with any groups the affinities of which can really be discussed. It is quite likely *a priori* that Jurassic mammals occurred in South America, but even if they were clearly identified, it is improbable that they would cast much light on the direct origins, geographic or taxonomic, of Tertiary taxa and faunas. Jurassic mammals of definite identification are known from North America, Europe, and Africa, and they do not cast much light on the Tertiary mammals of those continents. The only other South American mammal supposedly earlier than late Paleocene recently reported is the possibly Cretaceous *Perutherium* Grambast *et al.* (1967). It is clearly a primitive mammal, but both its age and its affinities are somewhat doubtful. It is almost certainly not a marsupial and evidently has no bearing on the argyrolagids.

itself, to the large body of evidence that Gondwanaland did not exist during those times and that continental drift did not then have any influence on land faunas and has little, if any, bearing on the present distribution of mammals. Whether Gondwanaland or continental drift or both occurred at earlier times and had some bearing on early Mesozoic and still older zoogeography is another matter, not relevant here.

BIOLOGY AND ECOLOGY

Function and convergence. As has become evident in previous pages, the argyrolagids present one of the most striking known examples of evolutionary convergence. Although there are more limited convergent resemblances to some other groups (e.g., to *Vombatus* in the dentition; to small macropodids in limb proportions and inferred locomotion), strongest convergence is with certain rodents: especially the kangaroo rats among the Heteromyidae (Dipodomyinae) and jerboas among the Dipodidae (Euchoreutinae, Allactaginae, and Dipodinae). For classification and figures of skulls and mandibles, see Ellerman (1940). For osteology see Lyon (1901), Hatt (1932), and Howell (1932; although only *Dipodomys* is mentioned in the title, comparisons with jerboas and illustrations of the latter are given throughout). My first-hand comparisons have been mostly with *Dipodomys merriami* and *Allactaga mongolica.* Over all, convergence has been stronger to the jerboas, but some characters are more like those of kangaroo rats.

The resemblance most obvious at first sight is in limb proportions and other characters associated in these living rodents, and therefore also by inference in the argyrolagids, with bipedal, ricochetal locomotion. There are, however, numerous other resemblances. Some of these, as in the masticatory apparatus, likewise can be ascribed with little doubt to similar functional adaptations. Others, such as the presence of palatal vacuities, have no functional significance evident to me, at least. They may, of course, have a common adaptive basis that I have failed to identify, or some may be coincidental, that is, may not have arisen by convergent adaptation to similar functions. There are nevertheless far too many resemblances to be entirely or to any great extent coincidental. Argyrolagids and the placental rodents toward which they converge (or which converge toward them) are only very distantly related and certainly had quite different ancestors. A common genetic basis, beyond that present in all Cenozoic Theria, cannot be involved; that is, this is a case in which convergence and parallelism can be clearly separated and the latter is ruled out. The resemblance between the kangaroo rats and the jerboas, here, incidentally involved, seems also to be largely convergent, but since both groups are rodents and probably had a common ancestor as late as the Eocene, a minor element of parallelism, i.e., of common genetic base for their specializations, may also be present.

In the dentition, resemblance of the argyrolagids is hardly more specific than to rodents in general: gnawing incisors; reduction of incisors, loss of canines, and reduction of premolars with development of a diastema; a grinding battery of a closed series of cheek teeth. The numbers of incisors and of cheek teeth are different. The cheek teeth resemble those of kangaroo rats in being rootless and wearing as quite simple prisms. Jerboas do develop somewhat heightened crowns but their teeth are rooted, subhypsodont at most, and somewhat, although not very much, more complex in pattern. The convergence here is just that the animals in question all have gnawing-grinding dentitions.

All three groups have rather long, narrow snouts. That is most marked in argyrolagids and resemblance is more to kangaroo rats than to jerboas. In argyrolagids the bony snout projects as a closed tube well in advance of the incisors; in *Dipo-*

domys it also projects well, but less than in argyrolagids, and it is open ventrally; in *Euchoreutes* it projects only slightly, and in *Allactaga* not at all. In *Allactaga* the incisive foramina are even larger and especially longer, proportionately, than in *Argyrolagus*. It is quite extraordinary that jerboas are among the few placentals that have palatal vacuities, quite large in *Euchoreutes*, for example (see Ellerman, 1940, fig. 150). They are even larger in *Argyrolagus*, but this is a convergent resemblance, and a baffling one. Such vacuities may be primitive for marsupials, but they have often been lost in that group; examples in South America are the Borhyaenidae, Necrolestidae, and some Caenolestoidea. These vacuities are not primitive for placentals and certainly evolved independently in the jerboas.

The remarkable orbital structure was stressed in the preceding anatomical description of *Argyrolagus* and some descriptive comparison was made with *Dipodomys*. The functional aspects can here be considered further and comparisons made with jerboas. In both kangaroo rats and jerboas the large eyeball is relatively posterior and does not fill the anterior part of the orbit. A temporal fossa is hardly distinguishable as such. These characters are carried to an extreme in *Argyrolagus*. In both of the recent groups the temporal muscle is greatly reduced and has a small origin, not on the cranium above the ear but almost on the posterior rim of the orbit. That must also have been true in *Argyrolagus*. In both kangaroo rats and jerboas the coronoid process on the mandible is correspondingly reduced, short anteroposteriorly and low vertically. It is likewise short in *Argyrolagus* and, although its height is not known, it must have been low, as inferred not only from analogy but also from the manifestly weak temporalis muscle and the lack of room posterior to the orbit.

The functional convergences in the anterior part of the orbit, although less obvious, are perhaps even more unusual. It has already been noted that the anterior part of the orbit is partly enclosed by bone dorsolaterally in *Dipodomys* and that a deep slip of the masseter originates here. In jerboas a much larger deep slip (or *masseter profundus*) originates anterior to the orbit proper and passes to insertion on the mandible posteroventrally through the greatly enlarged infraorbital foramen. In *Argyrolagus* almost exactly the same functional arrangement, correlated with reduction of postorbital jaw musculature and relatively posterior position of the eyeball, has evolved by expansion of the origin of a deep masseter *within* the orbit rather than through the infraorbital foramen. The position of that origin on the skull, the relative mass of the muscle, and its direction of pull on the mandible are similar in *Argyrolagus* and *Allactaga*. If one imagines the musculature unchanged in *Allactaga* but the infraorbital canal remaining primitive, the facial bones therefore covering the origin of the deep masseter, the resemblance to *Argyrolagus* would be very close.

All three of the groups here compared have rather short, broad, globular crania. All have epitympanic sinuses, probably in the mastoid in all three, and all have complete globular bullae, not homologous but functionally similar in *Argyrolagus* and the two groups of rodents. The extension or inflation of these cavities reaches great extremes in *Dipodomys* and some of the jerboas, e.g., *Scirtopoda*. It is moderate and closely similar in *Allactaga* and *Argyrolagus*. As has often been noted, the tendency for development and inflation of tympanic sinuses in recent mammals, mostly rodents, is especially common in arid and semiarid regions, although not confined to them. There has been long discussion of this point, some of it highly speculative but recently involving detailed experimentation and analysis. Webster (1961, 1962) has demonstrated for *Dipodomys* that the large middle-ear volume reduces damping

in the transmission of vibrations to the middle ear, produces resonance, and increases sensitivity to particular resonant frequencies. There is some evidence that the same effect occurs in *Meriones* (Legouix and Wisner, 1955), and it seems probable that it is general.

As far as I know, there are no data on the point, if any, at which middle-ear inflation becomes effective in producing resonance, and it is therefore uncertain whether this is an adequate explanation for the moderate inflation in *Argyrolagus*. A reasonable hypothesis might be that any development of a bulla (or hypotympanic sinus), an epitympanic sinus, or both, increases resonance proportionately and also is involved in the placing and height of peaks of sensitivity, in tuning the ear, so to speak. There would then presumably be an optimum degree of resonance and of flattening, peaking, and range of response toward which natural selection would bear in any given ecological situation.

For further understanding it would be necessary to know the adaptive significance of specific peak sensitivities, where these occur. Legouix, Petter, and Wisner (1954) suggested that in *Meriones* adaptation is for sensitivity to the cries of other individuals of the same species, thus promoting breeding in sparse, widely scattered populations. However, they presented no evidence that this does in fact occur. Webster (1962) has indicated that in *Dipodomys* intraspecific calls do not in fact occur in the range of most acute hearing. He demonstrated that auditory sensitivity in *Dipodomys* is crucial in evading predation in the dark by owls and rattlesnakes, which are in fact principal nocturnal predators on these rodents in nature. It does not follow that middle-ear inflation is always related to sounds produced by predators, but this is the only relationship that can now be considered definitely established. It also supports the more general proposition that inflated ears are tuned to a range in which there are environmental signals that affect survival of individuals or of species. (The facilitation of mating, if it occurs, would be within this category.)

Most recent mammals noteworthy for middle-ear expansion are also bipedal. An example additional to various rodents is provided by the elephant shrews (Macroscelididae). It has been suggested that ear specialization is related to equilibrium in these animals, but Webster's studies negate this. Nevertheless a relationship to ricochetal locomotion is indicated. Audition triggers an immediate leap into the air, and in Webster's experiments this was highly successful in thwarting the strike of a predator. Bartholomew and Caswell (1951) also noted it as the usual startle reaction in *Dipodomys*. Thus the two quite different morphological specializations are involved in a single behavioral adaptation. Although this has so far been demonstrated only for *Dipodomys*, it is a reasonable hypothesis, in the absence of evidence to the contrary, that it is also true of other saltatory mammals with expanded middle-ear cavities, including *Argyrolagus*. It is also relevant that most recent animals of this habitus are nocturnal or crepuscular. Although they tend to have large eyes with good light-gathering capacity, as did *Argyrolagus*, that habit would place a premium on audition as part of their defense mechanisms.[59]

[39] Although beside the present point, it may be of interest as a passing note that practically all early and the smaller later notoungulates, which were long the most abundant South American mammals, had notably expanded middle-ear cavities, with large epitympanic sinuses and bullae. In larger species these are not correspondingly enlarged but are relatively small although still present. These animals, even the small ones with proportionately enormous middle ears, were not bipedal but were cursorial. It is unlikely that their environments were arid or semiarid as a rule. It is also unlikely that many, if any, were nocturnal. They were evidently subject to heavy attack by a variety of predators, including large snakes. The large species must have been under less predation pressure.

In argyrolagids, kangaroo rats, and jerboas it is part of the bipedal adaptation that the pose of the head, indicated by the foramen magnum, condyles, and atlas, was at a marked angle to the neck.

In all three groups the symphysis of the mandible is unfused. All have reduced coronoid processes, as already noted. In *Argyrolagus* and jerboas, but not so much in kangaroo rats, the condyle (and correspondingly the glenoid surface on the skull) is little elevated above the level of the alveolar rim. In all there is a foramen and canal posterolateral to the last molar on the medial side of the anterior part of the base of the coronoid process. In *Allactaga* there are several openings in this area and another piercing the jaw posterior to the coronoid; this is not present in *Argyrolagus* or *Dipodomys*. Jerboas have a large, sometimes double masseteric foramen or vacuity in the mandible, somewhat similar to that of some phalangeroids. This is a verbal resemblance to *Argyrolagus*, but it is improbable that the small foramen of that genus is functionally similar. *Argyrolagus* has a fairly typical marsupial angular region and this does differ notably from that of generally convergent rodents. There is, however, some functional resemblance in the peculiar angular region of *Dipodomys*, in which the angle proper is strongly everted, somewhat like the masseteric crest of *Argyrolagus*, but also has a strongly inflected flange, somewhat like the angular process of *Argyrolagus* and most other marsupials.

Unfortunately, except for the not especially distinctive atlas we have no presacral vertebrae of *Argyrolagus* to compare with the columns of ricochetal rodents (see Hatt, 1932). *Argyrolagus*, *Dipodomys*, and *Allactaga* all have two similar fused sacral vertebrae entering into the sacroiliac joint, but in the last two there are two more fused sacrals or pseudosacrals posterior to those, and in *Argyrolagus* there are not. All three genera have very long and heavy tails, further similar in that proximal caudals with short centra, transverse processes, and traces, at least, of neural arches are abruptly followed by vertebrae with very long centra and no transverse processes or arches. Tails of this sort are an essential part of ricochetal adaptation, although, as has been noted, some evidently non-ricochetal forms, such as *Caenolestes*, have similar tails.[40]

Too little is known of the scapula of *Argyrolagus* for significant comparison. As noted in the anatomical section, the pelvis is markedly different from that of *Caenolestes*. It is functionally similiar to those of *Dipodomys* and *Allactaga*, especially the latter, which it more nearly resembles in the larger angle between the pubis and the ilium and in the larger symphysis, nearly parallel to the iliac-ischiac axis.[41] As pointed out in the anatomical section and shown in Table 3, the presacral extension of the ilium or, correspondingly, the relative approximation of acetabulum and sacrum seems to be a character of these bipedal ricochetal forms and is similar in kangaroo rats, jerboas, and *Argyrolagus*, but extreme in the latter.

Some limb measurements and proportions are given in Table 4 (p. 68). Most significant are the proportions there indicated by the ratios A/C and (A+B)/(C+D). Those show that in *Argyrolagus* and the bipedal ricochetal macropodids and rodents compared the humerus is less than half as long as the femur. The discrepancy in the second segments, ulnae and tibiae, is even greater. The great reduction in size of the

[40] I have not found a direct observation of locomotion in living caenolestids. Although their limb proportions and structures evidently exclude habitual bipedalism or ricocheting, it is entirely possible that they are effective hoppers.

[41] The specimen of *Allactaga mongolica* that I have used for most of these comparisons, Amer. Mus. Nat. Hist. No. 55978, male from "Ussuk," Mongolia, differs noticeably from that ascribed to the same species figured by Howell (1932, fig. 15A), but the differences in detail do not seem important for the present functional comparisons of distantly related animals.

foreleg and great increase in size of the hindleg would in itself force the conclusion that *Argyrolagus* was bipedal-ricochetal. It is true that the Australian dasyurid *Antechinomys*, which had for generations been described as bipedal because of the discrepant lengths of its fore and hind legs, has recently been shown by Ride (1965) to be quadrupedal with a true, but quite peculiar, gallop as its fast gait. That is, however, an exceptional case, and the over-all resemblance of *Argyrolagus* to the ricochetal rodents is closer than its resemblance to *Antechinomys*.[42] It is also of interest that Bartholomew and Caswell (1951) found that a species of *Dipodomys*, *D. panamintinus*, with a completely bipedal fast gait, also habitually uses a quadrupedal slow gait somewhat similiar to the quadrupedal fast gallop of *Antechinomys*. (Compare Bartholomew and Caswell, 1951, fig. 1, especially 1F, with Ride, 1965, fig. 1, especially 1.5.) Those authors found that another species of kangaroo rat, *D. merriami*, living in the same area is habitually bipedal even when moving slowly and rarely uses its forelegs in walking.

The ratio of humerus to radius in *Argyrolagus* is approximately as in recent caenolestids. In the macropodids and rodents compared the radius is relatively more elongated, but the difference is so little that it may have no functional significance. (Also note that these figures are estimates from incomplete bones, not precise measurements, in *Argyrolagus*.)

The humeri are generally similar in the three groups here especially compared, but *Dipodomys* and *Allactaga* both have the distal end of the deltoid crest produced into a strong tubercle, sharper and more definite than in *Argyrolagus*. The supinator ridge is somewhat higher and more flared in *Argyrolagus*. The humerus of *Argyrolagus* resembles that of *Dipodomys* in having an entepicondylar foramen and that of *Allactaga* in having a supratrochlear foramen. Radius and ulna are generally similar in form in the three genera.

Osgood (1921, p. 95) has shown that the tibia is longer relative to the femur in *Caenolestes* than in any other quadrupedal marsupial with which he compared it. The only strictly bipedal form compared was *Macropus giganteus*. As shown in Table 4, the most extremely bipedal of the recent forms compared, jerboas, have the tibia somewhat less elongate than the others, but the differences are hardly significant. Elongation is generally greater in bipeds, including *Argyrolagus*, than in quadrupeds, but the caenolestids are among a number of exceptions in the latter groups. It is somewhat unexpected that the metatarsus is not unusually elongated in at least some small macropodids. It is decidedly elongated in *Argyrolagus*, kangaroo rats, and jerboas. Elongation within the tarsal bones, which evolved at least three times independently in saltatory prosimians, is absent in this habitus (that is, the adaptive facies of *Argyrolagus* and its placental analogues).

The femora are generally similar in the three groups, but there are some differences the adaptive significance of which is not clear. The head, neck, and greater and lesser trochanters are functionally similar, and all have a strong, deep digital fossa, but in *Dipodomys* and *Allactaga* this extends obliquely to the base of the lesser trochanter and in *Argyrolagus* it extends straight distally, not near that base. *Argyrolagus* and *Dipodomys* have, but *Allactaga* lacks, a third trochanter. That of *Argyrolagus* is less sharp and produced, more proximal than that of *Dipodomys*. One would suppose that these differences would effect locomotion, but the bearing is not known and Howell (1932, p. 523) states in a categorical but, to me, somewhat puz-

[42] The Australian placental rodent (murid) *Notomys* is indeed bipedal-ricochetal (confirmed by Ride in the same brief published note) and is another of the numerous instances of association of that kind of locomotion with an inflated middle ear and an arid habitat.

zling way that the absence of a third trochanter in jerboas (and *Pedetes*) "has nothing to do with saltation."

The tibia and fibula are closely similar in all three groups, with no distinctions among these three of probable functional significance. Their great length and their fusion are saltatory specilizations.

The development of a true or pseudocannon bone is among the most striking features of the convergence, and especially interesting and characteristic of convergence from widely different ancestries in that it indicates close similarity in functional adaptation but is not morphologically homologous. In *Argyrolagus*, as described earlier, the pseudocannon bone consists of metatarsals III-IV and there are no other functional toes. In jerboas (except *Euchoreutes*) there is a triple cannon bone consisting of fused metatarsals II-III-IV. *Allactaga* generally retains digits I and V, but they are slender, short, and hardly functional. In *Dipus* and its closer relatives the lateral digits are completely suppressed, as in *Argyrolagus*.

Ecology. The convergences now discussed are so close and extensive that they must indicate similarities in adaptation and way of life, although doubts remain as to just how far such inferences can be carried. Several distinct but adaptively related functional systems are involved, especially: dentition and mastication, vision, hearing, and locomotion. Argyrolagid food habits were rodentlike and more specifically probably included mainly seeds and other nutritious parts of plants, and probably some insects, as is true of the most nearly similar living rodents. The large eyes, and indeed also the general habitus, suggest nocturnal and crepuscular activity. Auditory acuity was at least on the level of *Allactaga* but probably less peaked and less specialized for low frequencies than in most kangaroo rats. Locomotion was normally bipedal, although a facultative slow quadrupedal gait is not excluded; it was probably ricochetal at top speed; and it probably included a saltatory startle and defense reaction.

All living animals of this general adaptive type have ranges in semiarid to arid regions, although a few spread also into areas of greater rainfall and more vegetation, especially grasslands. Bartholomew and Caswell (1951) summarize the ecology of *Dipodomys* in part as follows:

"Except in a few instances the genus *Dipodomys* inhabits regions characterized by a lack of continuous plant cover. . . . The problem of escaping predators is not one of sustained high-speed locomotion, but one of quick-starting evasive locomotion in open terrain over short distances. . . . This rodent can be expected to occupy successfully only those regions in which smooth-surfaced, sparsely-vegetated foraging areas are available. These areas need not, however, be extensive."

It is a further element of this adaptive system that the animals live in burrows and have a restricted feeding range, mainly across open ground, around the burrow. Similar habits are reported for jerboas (e.g., Feniuk and Kazantzeva, 1937).

Recent rodents of this habitus also have some striking physiological adaptations. For example, kangaroo rats and jerboas can live indefinitely without drinking and have highly concentrated urine. (See Schmidt-Nielsen, 1964, for these and other physiological adaptations.) It would be carrying serious paleobiological inference too far to assume that argyrolagids had similar physiological adaptations to arid environments, but it is an interesting speculation.

The faunal associations of argyrolagids give some additional evidence as to ecology. The Chapadmalal Formation, as restricted, has relatively abundant argyrolagids (they are everywhere far from absolute abundance) and has a rich, adequately identified, definitely associated fauna, listed by Reig (1958). The fauna suggests a predominance of open grassland.

There was certainly abundant food for grazers and browsers. Truly arid or desert conditions seem to be ruled out, but semiarid conditions, relatively open and with some bare soil, more or less as in the southern pampas and much of Patagonia today, are quite possible. There are no definitely arboreal animals, although a few, such as the fairly common didelphids, could possibly have been arboreal. The predominant faunal elements are edentates and rodents, consistent with semiarid grassland and brushland (*pampa* and *mata*). The less common ungulates include probable browsers and grazers, as well as a peccary (*Platygonus*). Recent peccaries are remarkably eurytopic and euryokous, ranging from the equator far into the Temperate zones and from rain forest to full desert, and the Chapadmalal ungulates (as well as some other mammals) may well have been also. The presence of fairly common remains of leptodactylid frogs and of capybaras, and indeed also of so many other animals, indicates the presence of water, probably but not necessarily perennial streams.

Other faunas associated with argyrolagids are not so well documented, and at Monte Hermoso and in Catamarca the precision of association is uncertain. However, the probable associations and ecologies are generally similar to those in the Chapadmalal Formation. Rather cursory studies of sedimentation do not as yet add significantly to the ecological picture.

There is a fair probability that the principal peculiarities of the argyrolagids evolved as adaptations under desert conditions. If so, their known occurrences are in ecologies still appropriate for them but probably less extreme than the ancestral environments primarily responsible for their specializations or marginal to those environments. Ancestral stenoky in localized environments little or not represented in the known fossil record could also bear on the late appearance of this group in that record and its appearance in already fully specialized form.[43]

Extinction. It is well-known that extinction rates of mammals throughout the world were high in the Pleistocene and immediate post-Pleistocene. It has further often been pointed out that in this episode large mammals were much more liable to extinction than small. Innumerable causes for those extinctions and for the size differential have been postulated. Gill (1955), referring to Australian marsupials, suggested that although some concomitants of gigantism had a powerful effect, it was not the sole cause, that each case of extinction must be judged separately, that causes were multiple, and that they included psychological and physiological characters not now determinable. Martin (1958, 1966) believes that the primary cause was human predation, with overkill on the larger species. Axelrod (1967) has returned to the classical theory, which dates back at least to Lyell early in the nineteenth century, that the primary cause was change in climate, especially, in Axelrod's form of the theory, as increasingly inequable climates affected reproduction, vegetation, and other ecological necessities.[44] He supposes that small mammals survived because they had protected homes, stored food, and mated in spring.

The Argyrolagoidea present an extraordinary exception in that a whole major group of quite small mammals became extinct during the Pleistocene. By all rules of analogy and theories of extinction, they should have survived, as did their close ecological analogues in North America, Asia, Africa, and Australia. They cannot be brought under any theory of differential extinction more explicit than Gill's view that extinction of some of the argyr-

[43] For a general discussion of stenoky and euroky see Allee, Park, Emerson, Park, and Schmidt (1949), especially pp. 206–215.

[44] Note a misprint in Axelrod's paper important to his thesis. Page 32, line 4, for "equability" read "inequability."

olagids' distant relatives in Australia had a combination of causes some of which are unknowable. The case is made more striking by these facts: no other adaptively or ecologically similar animals survived (or ever occurred) in South America, as far as we know; the abundant adaptively and ecologically similar pocket mice and kangaroo rats of North America never spread into South America or competed with the argyrolagids; and South America still has habitats and communities ecologically similar to those in which adaptive analogues of the argyrolagids survived and are still abundant on other continents.[45]

If local arid-semiarid areas ecologically suitable for argyrolagids had gone through a geologically brief episode of greater precipitation, and especially if they had become forested even for a century or so, the resident argyrolagids would have become maladapted and probably extinct. There is, however, no evidence known to me that such an episode occurred.

CONSPECTUS OF SOUTH AMERICAN MARSUPIALS

New knowledge of the argyrolagids emphasizes and extends the evidence that adaptive radiation of marsupials in South America has been even more extensive than is usually realized.

Historical note. Following, with modification, an earlier concept of T. H. Huxley's, Ameghino considered Metatheria (Marsupialia) and Eutheria (Placentalia) as successive evolutionary levels or grades, not as phylogenetic clades (in later nomenclature). Those groups therefore do not appear as taxa in Ameghino's developed classifications. The vernacular term "marsupial" (in French or Spanish) was used, but mostly in a sense descriptive of supposed earlier stages in the ancestry of placentals. Ameghino's classification of 1906 placed what we now classify as fossil South American marsupials in eight major taxa (mainly orders, although the categorical level is not always clear): Allotheria, Paucituberculata, Pedimana, Insectivora, Sparassodonta, Creodonta, Prosimiae, and Protungulata. Within these, 17 families were based on forms now considered marsupial, and marsupials were erroneously referred to four non-marsupial families. In addition, one family (Odontomysopidae) was placed in association with marsupials but was based on specimens of unidentifiable affinities. Ameghino believed that most placentals were derived independently from one or another of these families, specifying insectivores, carnivores, lagomorphs, rodents, ungulates, and primates.

Even early while Ameghino was working, it was realized by others that many of the groups here in question were marsupials in a phylogenetic sense and not stages in the ancestries of various placentals. Thus in his pioneering textbook Smith Woodward (1898) indicated that Ameghino's four families of Paucituberculata represent one or more families of Marsupialia. He also commented on the "very remarkable" resemblance of Ameghino's Sparassodonta (eventually with 6 families) to the carnivorous marsupials of Australia, but referred them to the suborder Creodonta of the placental order Carnivora.

The major clarification was made by Sinclair (1906) in a monograph coincidentally published at almost the same time as Ameghino's main synthesis of Argentine faunas and mammalian phylogeny. Sinclair showed that almost all the mid-Tertiary (Santacrucian) representatives of Ameghino's numerous orders and families referred to above belong to just three natural groups, each referable to a single family: Ameghino's Sparassodonta, placed by Sinclair in an Australian family (or, as I prefer, subfamily) with *Thylacinus* but now always given family distinction as

[45] Because there is no apparent reason why argyrolagids should be extinct, the thought arises that perhaps they are not. However, collection of even small, obscure mammals in South America is now so intensive that this is a forlorn hope.

Borhyaenidae; Ameghino's Paucituberculata, placed in the Caenolestidae; and Ameghino's Pedimana, placed in the "Didelphyidae" (i.e., Didelphidae).

Genera referred by Ameghino to the Allotheria, absent from the middle (and later) Tertiary and not considered by Sinclair, were later shown to represent a single distinctive marsupial family, Polydolopidae, allied to the Caenolestidae (Gregory, 1910; Simpson, 1928, 1948). The situation has further been tidied up bit by bit by showing that various others of Ameghino's marsupial, or supposedly marsupial-like, taxa either are invalid or belong in one or the other of the four families so far indicated: Didelphidae, Borhyaenidae, Caenolestidae, and Polydolopidae. The Caroloameghiniidae, referred by Ameghino to the Protungulata, are closely related to the opossums (Scott, 1937; Simpson, 1948), and I would now place them as a subfamily of Didelphidae.[46] As noted above, the "Odontomysopidae," placed by Ameghino in the Allotheria, are unidentifiable, probably not marsupials (Simpson, 1967). *Anissodolops*, placed by Ameghino in the multituberculate family Neoplagiaulacidae, is a synonym of *Polydolops* and of course belongs in the Polydolopidae (Simpson, 1948). *Argyrolestes* and *Nemolestes*, placed by Ameghino in the Jurassic family Spalacotheriidae, which he erroneously considered Insectivora, belong in the Borhyaenidae (Simpson, 1948). In Ameghino's Prosimiae, the Clenialitidae and *Pitheculites*, referred to the Homunculidae (which are Primates), are *incertae sedis* but could belong to the Caenolestidae (Bluntschli, 1931). Sinclair (1906) had already shown that *Acrocyon*, referred by Ameghino to the Creodonta, belonged in the vicinity of *Borhyaena*, hence in the Borhyaenidae of current classifications.

Thus almost all of Ameghino's taxonomy was cleared up, and considerations of marsupial evolution in South America have generally been in terms of the four families specified above that are, so to speak, residual from Ameghino's classification. However, Patterson (1958) has shown that the Necrolestidae, sole genus *Necrolestes*, referred by Ameghino, Scott, and others to the Insectivora, are a highly distinctive, valid family of Marsupialia, and Patterson (1952) also added another very distinctive family, Groeberiidae, based on a specimen found after Ameghino. The situation has been further modified by important discoveries belonging to known families: the extremely distinctive subfamily Thylacosmilinae, family Borhyaenidae (Riggs, 1934); a polydolopid and remarkably varied Paleocene didelphids in Brazil (Paula Couto, 1952, 1962); and the argyrolagids described in this contribution. Less extraordinary but also adding significantly to the total knowledge of South American marsupials have been many other finds and studies, too numerous to specify here; Reig (1958b) and Ringuelet (1953) may be mentioned as examples.

Review of known groups. The supergeneric taxa[47] now recognized and their known geologic range in South America are as follows:

Didelphoidea
  Didelphidae
    Didelphinae. Late Paleocene—Recent.
    Caroloameghiniinae. Early Eocene.
    Sparassocyninae. Middle Pliocene—Early Pleistocene.
  Borhyaenidae
    Borhyaeninae. Late Paleocene—Pleistocene.

[46] In agreement with Clemens (1966), a conclusion I had independently reached but not published.

[47] No engagement is given that any of these family-group names are valid under the present code, and some probably are not. They are, however, the names usual, practically universal, in recent literature and most readily understood by any present student of marsupials or mammals in general. The very extensive, unproductive bibliographic labor that would be necessary to determine the names most likely to be valid is not part of the present research plan.

Thylacosmilinae. Pliocene—Early Pleistocene.
Necrolestidae. Early Miocene.

Caenolestoidea
Caenolestidae
Caenolestinae. ?Early Eocene—Recent.
Palaeothentinae. Early Oligocene—Early Miocene.
Abderitinae. Early Oligocene—Early Miocene.
Polydolopidae. Late Paleocene—Early Eocene.
Groeberiidae. Early Oligocene.

Argyrolagoidea
Argyrolagidae. Late (?Middle) Pliocene—Early (?Middle) Pleistocene.

There are still a few South American fossils, more or less definable at lower taxonomic levels, that are of uncertain supergeneric affinities and might prove to be marsupials. Perhaps the most likely of these is *Gashternia* Simpson, 1935 (see Simpson, 1948, p. 69; Clemens, 1966, p. 33).

The recognized families and subfamilies, with the sole exception of Didelphidae, Didelphinae, are known only from South America. They almost certainly originated on that continent and probably have always been endemic there. Didelphinae are also known from the late Cretaceous of North America and the Paleocene to Miocene of North America and Europe. They reappeared in the Pleistocene of North America, apparently as immigrants from South America, and although they are the most primitive of all known marsupials, they survive on both continents. There is no direct evidence as to where they originated and South America is not ruled out, but indirect evidence makes origin somewhere in Holarctica seem more probable. Early didelphines were probably ancestral to all other South American marsupials. No identifiable marsupials earlier than the late Paleocene have yet been found in South America, but the already marked differentiation of marsupials at that time implies long post-didelphine evolution. Didelphines, wherever they came from, were almost certainly already present in South America in the late Cretaceous.

Forms transitional between didelphines and borhyaenines were still present in the late Paleocene, although some primitive borhyaenines were also already in existence. In no other case are intermediates between ancestral didelphines and more specialized subfamilies or families known. In each instance, including even the more specialized subfamilies of Didelphidae and Borhyaenidae, the advanced groups appear in the record with their essential specializations already present. It is also noteworthy that most of the specialized groups have short records, although they must have been in existence over much longer periods of time. The Caroloameghiniinae, Necrolestidae, and Groeberiidae are each known from only one geological formation. The Sparassocyninae, Thylacosmilinae, Polydolopidae, and Argyrolagidae are each known from only two or three successive formations or ages, with known spans shorter than an epoch.

Those facts emphasize the incompleteness of the South American fossil record in general. They also suggest that major parts of marsupial evolution were occurring in areas and facies inadequately sampled, if at all, by the known fossil deposits and the collections so far made. In fact before the middle to late Pleistocene most of the faunas reasonably well known are from quite restricted areas for any one age, many such areas are marginal on the continent, and some, at least, of the faunas are of peculiar and limited facies. Didelphidae are quite rare or absent in most known local faunas, but happen to be dominant faunal elements at Itaborai (late Paleocene, Brazil) and in Bed 9 of the Chapadmalal Formation (early Pleistocene, Argentina, also an argyrolagid facies). Groeberiidae are known from only one small exposure and in a very peculiar

faunal facies (see Simpson, Minoprio, and Patterson, 1962). A complete record of South American marsupials would certainly include a large number of taxa, probably some of high categorical rank, now unknown.

Although the radiation of marsupials in South America was doubtless more extensive than is yet known, the radiation demonstrated by the incomplete record is impressive. It is only a little less extensive than the radiation in Australia, and in that respect South America was also a land of marsupials. Convergence and parallelism between the two radiations did occur, but there are also some striking differences. The South American groups will be briefly characterized under family headings.

DIDELPHIDAE. This family is defined to include a large number of genera and species which, although very diverse, did not diverge so much from primitive marsupial morphology as to require higher categorical rank. The family is thus conservative by definition, but the fact that even now in the Recent there are taxa fulfilling that definition indicates remarkable conservatism and low evolutionary rate.[48] The family as a whole is omnivorous and individuals are usually highly adaptable (or euryokous in ecological terms), but some species and individuals have more limited diets and habits. Many of the smaller South American species probably had more or less insectivore-like habits. (The only member of the Insectivora known ever to have occurred in South America is a recent immigrant in the far north.) Among the already highly varied, yet not markedly different, late Paleocene didelphids in the Itaborai Paleocene is *Derorhynchus*, especially insectivore-like, with a long symphyseal region and procumbent incisors and canine. In connection with it, Paula Couto remarked, "It seems to us, then, that the insectivorous didelphids along with the Caenolestoidea as a whole played the same role as the Insectivora in South America Tertiary ecology, as is true of the recent *Caenolestes*" (Paula Couto, 1962, p. 147).[49] It is probable that some of those Paleocene genera, when better known, will already justify subfamily separation. However, in view of didelphid diversity, I do not now, as formerly, distinguish the microbiotheres at that level. They are more like didelphines than the subfamilies clearly requiring designation as such. In South America, the latter are the early Caroloameghiniinae (Simpson, 1948), bunodont and multicuspid, and the later Sparassocyninae, peculiar for short, heavy skulls with epitympanic sinuses and somewhat specialized dentition (Reig, 1958b).[50]

BORHYAENIDAE. For unknown reasons, subject to speculation and hypothesizing

[48] There are indeed distinct differences between the known Cretaceous marsupials and any Recent members of the order, as noted especially by Clemens (1966). However, reference by Clemens and others of some Cretaceous and Recent forms to the same subfamily, Didelphinae, recognizes extraordinary conservatism, much greater than is demonstrable for any other mammals.

[49] "Nos parece, pues, que los didelfídeos insectívoros, juntamente con los Caenolestoidea en general, desempeñaron el mismo papel que los Insectivora en la ecología del Terciario sudamericano, como sucede con los actuales *Caenolestes*." It may be added that recent caenolestids are confined to limited Andean areas and that the roles of Insectivora in most parts of South America are now played by small didelphids and some small rodents.

[50] The Cretaceous didelphoids from North America show a degree, although only in part a kind, of diversity comparable to that now known for Paleocene-Eocene South American didelphoids. In Clemens's (1966) excellent study of these with greatly augmented materials, he has raised two former subfamilies of Didelphidae to the rank of families, his Pediomyidae and Stagodontidae. If *Derorhynchus* and some other peculiar Paleocene South American genera and also, as Clemens agrees, *Caroloameghinia* and *Glasbius* (Clemens's genus from North America) are retained in Didelphidae, I think that *Pediomys* and *Didelphodon* (essentially the type of Stagodontidae despite the difference in names) likewise warrant no more than subfamily distinction. This is a minor point, but it has some importance in maintaining a reasonable balance of categorical levels.

not especially pertinent in this study, no placental carnivores appeared in South America until the late Pliocene. However, carnivorous marsupials were becoming differentiated from the didelphids in the Paleocene. In the Eocene they were already quite diverse and included definitely predaceous types. Some of the didelphids, strictly speaking, doubtless also included small live prey in their diets, as do a number of recent didelphines. In the middle and later Tertiary the borhyaenids had a large range in size and also in the extent and details of carnassial specialization. Between them and some didelphids, the ecological niches for carnivores seem to have been about as full as in North America or the Old World except Australia, and rather more so than in Australia. Most aberrant and remarkable were the thylacosmilines, convergent in great detail to the placental sabertooths, a habitus that never evolved in Australia as far as known.

Necrolestidae. This family, unquestionably valid as such, is known by a single genus, probably a single species, and very few specimens. It is another vicar for insectivores, lacking as such in a phylogenetic sense in the South American faunas. It is closely convergent to the marsupial "mole," *Notoryctes*, of Australia and to the placental golden "moles," Chrysochloridae, of Africa. (Besides Patterson, 1958, see Scott, 1905.) Convergence to the true moles, Talpidae, of Eurasia and North America is not quite so close, but the ecological similarity is still great. Animals of similar adaptive facies survive on all other continents under climatic, edaphic, and community conditions present in South America, but there is nothing like it in South America now. This is another family, like the argyrolagids, that apparently should have survived. But it did not.

Caenolestidae. The Caenolestinae, only surviving group, are diminutive animals with procumbent, pinching incisors and broadly insectivore-like cheek teeth. They are in fact insectivorous and evidently have shared that facies with some didelphids throughout the Cenozoic in South America.[51] The Palaeothentinae and Abderitinae differ mainly in progressively greater development of shearing action in a cheek tooth immediately anterior to the triturating molars. This, with the Polydolopidae (below), represents rather close convergence in dentition (but not other anatomical features) to the "rat" kangaroos (bettongs, tungoos, squeakers, potoroos, etc., Potoroinae) of Australia, also to the phalangerid *Burramys*, most multituberculates, and some primates (see Simpson, 1933). The recent marsupials with such "plagiaulacoid" dentitions are all herbivores, and it has been inferred that the fossil animals of this facies but other taxa were also. They may, however, be some question as to where or whether in the caenolestoid series transition from insectivorous to herbivorous habits occurred. If it did occur, the specialized caenolestoids were ecologically more like some small rodents than like insectivores. All of them evolved before there were any Rodentia in South America. The polydolopids apparently became extinct before they had rodent competitors, but the Palaeothentinae and Abderitinae lived for a long time (at least Deseadan through Santacrucian) in communal associations with rodents.

Polydolopidae. These animals represent the extreme of "plagiaulacoid" specialization in the caenolestoids, discussed above. Primitive conditions in a Paleocene polydolopid from Itaborai suggested to Paula Couto (1952) that the principal lower shearing tooth is not homologous in Polydolopidae and specialized Caenolestidae (mainly Abderitinae), although he continued to accept caenolestoid affinities for

[51] Armadillos, also present from the Paleocene onward, are also largely insectivorous, and anteaters, from the mid-Tertiary, are exclusively so but with much more stringent restriction among insect prey. Thus although lacking Insectivora, South America has long had a full complement of insectivores.

the former. That has been generally accepted, by me among others, but on second thought I think that this evidence does not necessarily negate homology of the shearing teeth. In any case, whether independently evolved or not, the Polydolopidae do represent in more extreme form an adaptive trend, and hence probably an ecological habitus, exhibited in less specialized form in the Palaeothentinae and Abderitinae.

GROEBERIIDAE. The one, poorly known species is decidedly rodent-like in the lower jaw and dentition (Patterson, 1952). It is perhaps significant that placental rodents are not known in the same fauna, which may possibly antedate the arrival of rodents in that region (Simpson, Minoprio, and Patterson, 1962). In any case, the origin of the Groeberiidae almost certainly occurred in the absence of Rodentia, and rodent competition could conceivably account for their extinction. However, they lived under ecological conditions evidently quite peculiar, although in an unknown way, and may have survived for some time, as they originated, without presently known record.

ARGYROLAGIDAE. This family needs no further characterization at this point. The purpose of the present conspectus is to show how wide was the adaptive radiation and ecological dispersal of marsupials in South America and that the argyrolagids add an evolutionary development that was markedly distinct, not only phylogenetically, but also adaptively and ecologically.

Faunal comparisons. In Tertiary South America, marsupials underwent a wide adaptive radiation that fitted them into some ecological roles played by placentals in all other continents with the incomplete exception of Australia. They occupied all the usual roles for carnivores, including the extreme sabertooth habitus (Thylacosmilinae) most of those for insectivores, including the extreme fossorial habitus (Necrolestidae), and some of those for rodents, including the extreme ricochetal habitus (Argyrolagidae). Also included were the extraordinarily adaptable didelphids, ranging from insectivorous to carnivorous, to frugivorous, or generally polyphagous. They have had a talent for survival and are, in fact, the only American marsupials that do survive except for a few, also rather generalized caenolestids.

That wide radiation took place in communities that also included even more numerous and more varied placentals. In ecologically balanced marsupial-placental faunas, roles were divided between those groups and the radiation of each was limited thereby. Marsupials did not evolve into fully herbivorous browsers and grazers, those niches being divided among the very numerous ungulates and some of the edentates. Marsupials never attained anything approaching the breadth and diversity of rodent adaptations, those being occupied early in part by small ungulates and later in enormous variety by rodents themselves. Arboreal insectivorous-frugivororus habits evidently occurred among some didelphids, and I suspect may have involved some more early specialized extinct marsupials not yet found or not recognized as belonging in these niches. These niches later were largely taken over by primates. Terrestrial insectivorous niches were divided among marsupials and edentates, as most of them still are.

In Australia, balanced mammalian faunas evolved with much less placental participation, and the parallel between marsupial radiations in Australia and South America is limited by that fact. Bats are abundant in Australia and are inferred to have been so for a long time, as also in South America. Although there are gliding phalangeroids in Australia,[52] no known marsupials anywhere are really batlike. Rats (Muridae) have long been numerous and varied in Australia, and this seems to have inhibited the evolution, or survival, of ratlike mar-

[52] It is curious that South America, with its great and varied forests, has no gliding mammals. It is the only continent without them.

supials since the Miocene, at least. There are, however, rodentlike, non-ratlike marsupials such as *Vombatus*. There are somewhat *Vombatus*-like true rodents in South America, but no marsupials of similar habitus. In over-all habitus the South American argyrolagids are more like the Australian placental *Notomys* than like any Australian marsupials, although there is some slight resemblance to small macropodids and, still more distantly, even to some peramelids. As noted above, insectivorous marsupials have been common in South America throughout the Cenozoic but have shared insect food with a number of placentals. In Australia most of the small dasyurids are at least partly insectivorous, and some are ecologically quite similar to small didelphids. One, the numbat (*Myrmecobius*), is a specialized anteater. (As with so-called anteaters in South America, numbats probably eat more termites than ants.) Even with the addition of the monotreme anteaters, these animals may never have been really abundant or diverse, and they do not balance the more common and highly varied ant and termite eaters in South America.[53] Bandicoots (Peramelidae) are also partly insectivorous in a broad sense, although it is not evident that many of them depend entirely on insect food.

The major difference between South American and Australian marsupial radiations is that in South America all the medium-sized to large herbivores, including strict browsers and grazers, have been placentals throughout the Cenozoic whereas in Australia they have all been marsupials. In both faunas these animals have been among the most individually abundant and taxonomically varied, so that the faunas over-all have been and are very different in aspect in spite of the fact that both embrace wide-ranging marsupial radiations. The contrast is heightened by the fact that the Australian marsupial and the South American placental herbivores exhibit very little morphological convergence, although they have similar ecological roles.

[53] This rich food source is not exploited entirely by mammals in any region. Reptiles, birds, and often still other groups also share.

Numbats are now extinct over much of their range and are rapidly diminishing over the rest of it. This is largely, perhaps entirely, caused by human activities, not by direct onslaught but from modification of the environment, especially by bush fires (Wood Jones, 1923, pp. 126–127). This has a particular interest in that it shows that small, non-prey animals, exempted by Martin (e.g., 1958, 1966) from his general theory of human intervention as cause of Pleistocene-Recent extinction, can also be affected.

Wood Jones's classic account (*loc. cit.*) should be modified on two points: the statement that numbats are "probably phylogenetically senile" is meaningless in the light of present knowledge of adaptation and evolution; the quotation without dissent of a here anonymous opinion that *Myrmecobius* is actually an unmodified survivor of Jurassic marsupials is doubly wrong—there were no Jurassic marsupials, and *Myrmecobius* is not an unmodified, or even a moderately modified survivor of any Jurassic mammals.

LITERATURE CITED

Allee, W. C., Orlando Park, Alfred E. Emerson, Thomas Park, and Karl P. Schmidt. 1949. Principles of Animal Ecology. Philadelphia and London, W. B. Saunders Company.

Ameghino, Carlos. 1904, 1936. Letter in F. Ameghino, 1913–1936, Vol. **22** (1936), pp. 19–20.

Ameghino, Florentino. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Acta Acad. Nac. Cien. Córdoba, **6**:i–xxxii, 1–1027, and atlas.

———. 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el eoceno inferior de la Patagonia austral. Especies nuevas, adiciones y correcciones. Rev. Argentina Hist. Nat., **1**:289–328.

———. 1903–1904. Nuevos especies de mamíferos cretáceos y terciarios de la República Argentina. An. Soc. Cien. Argentina, **56**:193–208 (1903); **57**:162–175, 327–341; **58**:35–71, 182–192, 225–291. Also a separate, published in 1904, pp. 1–142. Again published, again with new pagination, in the *Obras* (Ameghino, 1913–1936, **15**:95–218).

———. 1906. Les formations sédimentaires du Crétacé supérieur et du Tertiaire de Patagonie. Ann. Mus. Nac. Buenos Aires, (3)**8**: 1–568. Also published, with Spanish trans-

lation, as volume 16 of the *Obras* (Ameghino, 1913–1936).

———. 1912. L'age des formations sédimentaires tertiaires de l'Argentine en rélation avec l'antiquité de l'homme. Note supplémentaire. An. Mus. Nac. Buenos Aires, **22**:169–179. Also in the *Obras* (Ameghino, 1913–1936, **18**:602–621) with Spanish translation.

———. 1913–1936. Obras completas y correspondencia científica de Florentino Ameghino. A. J. Torcelli, ed. 24 vols. Edición Oficial, La Plata, Argentina.

AXELROD, DANIEL I. 1967. Quaternary extinctions of large mammals. Univ. California Pub. Geol. Sci., **74**:1–42.

BARTHOLOMEW, GEORGE A., JR., AND HERBERT H. CASWELL, JR. 1951. Locomotion in kangaroo rats and its adaptive significance. Jour. Mammal., **32**:155–169.

BLUNTSCHLI, HANS. 1931. *Homunculus patagonicus* und die ihm zugereihten Fossilfunde aus den Santa-Cruz-Schichten Patagoniens. Morphol. Jahrb., **67**:811–892.

BUTLER, PERCY M., AND A. TINDELL HOPWOOD. 1957. Insectivora and Chiroptera from the Miocene rocks of Kenya Colony. British Mus. (Nat. Hist.), Fossil Mammals of Africa, No. **13**:1–35.

CAMP, C. L., AND V. L. VANDERHOOF. 1940. Bibliography of fossil vertebrates 1928–1933. Geol. Soc. Amer., Special Papers, No. **27**.

CASAMIQUELA, RODOLFO M. 1961. Sobre la presencia de un mamífero en el primer elenco (icnológico) de vertebrados del Jurásico de la Patagonia. Physis, **22**:225–233.

CASTELLANOS, ALFREDO. 1934. Conexiones sudamericanas en relación con las migraciones humanas. Quid Novi?, 2, No. 6 (consulted as a separate, pp. 1–11).

CLEMENS, WILLIAM A., JR. 1966. Fossil mammals of the type Lance formation, Wyoming. Part II. Marsupialia. Univ. California Pub. Geol. Sci., **62**:1–122.

DEDERER, PAULINE H. 1909. Comparison of *Caenolestes* with Polyprotodonta and Diprotodonta. Amer. Nat., **43**:614–618.

ELLERMAN, J. R. 1940. The Families and Genera of Living Rodents. Vol. I. Rodents other than Muridae. British Museum (Nat. Hist.), London.

FENIUK, B. K., AND J. M. KAZANTZEVA. 1937. The ecology of *Dipus sagitta*. Jour. Mammal., **18**: 409–426.

GILL, EDMUND D. 1955. The problem of extinction with special reference to Australian marsupials. Evolution, **9**:87–92.

GRAMBAST, L., M. MARTINEZ, M. MATTAUER, AND L. THALER. 1967. *Perutherium altiplanense* nov. gen., nov. sp., premier mammifère mésozoïque d'Amérique du Sud. Comptes Rendus Acad. Sci., **264**:707–710.

GREGORY, WILLIAM K. 1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., **27**: 1–524.

HATT, ROBERT T. 1932. The vertebral columns of ricochetal rodents. Bull. Amer. Mus. Nat. Hist., **63**:599–738.

HOWELL, A. BRAZIER. 1932. The saltatorial rodent *Dipodomys*: the functional and comparative anatomy of its muscular and osseous systems. Proc. Amer. Acad. Arts Sci., **67**: 377–536.

JONES, FREDERIC WOOD. 1923, 1924. The Mammals of South Australia. 2 vols. Adelaide, Government Printer.

KRAGLIEVICH, JORGE LUCAS. 1952. El perfil geológico de Chapadmalal y Miramar, Provincia de Buenos Aires. Rev. Mus. Municipal Cien. Nat. y Tradic. Mar del Plata, **1**:8–37.

KRAGLIEVICH, LUCAS. 1931. Cuatro notas paleontológicas, sobre *Octomylodon aversus* Amegh., *Argyrolagus palmeri* Amegh., *Tetrastylus montanus* Amegh., y *Muñizia paranensis*. Rev. Soc. Argentina Cien. Nat., **10**:242–266. Also in the *Obras* (Kraglievich, 1940, pp. 581–602).

———. 1934. La antigüedad pliocena de las faunas de Monte Hermoso y Chapadmalal, deducidas de su comparación con las que le precedieron y sucedieron. Montevideo, El Siglo Ilustrado.

———. 1940. Obras de Geología y Paleontología. A. J. Torcelli and C. A. Marelli, eds. Vol. 2. Ministerio de Obras Públicas de la Provincia de Buenos Aires, Buenos Aires, Argentina.

LEGOUIX, J. P., F. PETTER, AND A. WISNER. 1954. Étude de l'audition chez des mammifères à bulles tympaniques hypertrophiées. Mammalia, **18**:262–271.

LEGOUIX, J. P., AND A. WISNER. 1955. Rôle functionel des bulles tympaniques géantes de certains rongeurs (*Meriones*). Acustica, **5**: 209–216.

LYON, M. W., JR. 1901. A comparison of the osteology of the jerboas and jumping mice. Proc. U. S. Nat. Mus., **23**:659–668.

MARTIN, PAUL S. 1958. Pleistocene ecology and biogeography of North America. *In*: C. Hubbs (ed.), Zoogeography, Amer. Assoc. Adv. Sci., Spec. Pub. No. 51, Chapter 15.

———. 1966. Africa and Pleistocene overkill. Nature, **212**:339–342.

OSBORN, HENRY FAIRFIELD. 1910. The Age of Mammals in Europe, Asia and North America. New York, Macmillan.

OSGOOD, WILFRED H. 1921. A monographic study

of the American marsupial *Caenolestes*. Pub. Field Mus. Nat. Hist., Zool., **14**:1–162.

———. 1924. Review of living caenolestids with description of a new genus from Chile. Pub. Field Mus. Nat. Hist., Zool., **14**:165–172.

Patterson, Bryan. 1952. Un nuevo y extraordinario marsupial deseadiano. Rev. Mus. Municipal Cien. Nat. y Tradic. Mar del Plata, **1**:39–44.

———. 1958. Affinities of the Patagonian fossil mammal *Necrolestes*. Breviora, No. **94**:1–14.

———. 1965. The fossil elephant shrews (Family Macroscelididae). Bull. Mus. Comp. Zool., **133**:295–335.

Paula Couto, Carlos de. 1952. Fossil marsupials from the beginning of the Cenozoic in Brazil. Marsupialia: Polydolopidae and Borhyaenidae. Amer. Mus. Novit., No. **1559**: 1–27.

———. 1962. Didelfídeos fósiles del Paleoceno de Brasil. Rev. Mus. Argentino Cien. Nat. "Bernardino Rivadavia," Cien. Zool., **8**:135–166.

Reig, Osvaldo A. 1955. Un nuevo género y especie de cenolestinos del Plioceno de la provincia de Buenos Aires (República Argentina). Rev. Asoc. Geol. Argentina, **10**:60–71.

———. 1958a. Notas para una actualización del conocimiento del la fauna de la formación Chapadmalal. I. Lista faunística preliminar. Acta Geol. Lilloana, **2**:241–253.

———. 1958b. Notas pora una actualización del conocimiento de la fauna de la formación Chapadmalal. II. Amphibia, Reptilia, Aves, Mammalia (Marsupialia: Didelphiidae, Borhyaenidae). Acta Geol. Lilloana, **2**:255–283.

Ride, W. D. L. 1964. A review of Australian fossil marsupials. Jour. Roy. Soc. Western Australia, **47**:97–131.

———. 1965. Locomotion in the Australian marsupial *Antechinomys*. Nature, **205**:199.

Riggs, Elmer S. 1934. A new marsupial sabertooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. Trans. Amer. Phil. Soc., new ser., **24**:1–31.

Ringuelet, A. B. de. 1953. Revisión de los didélfidos fósiles argentinos. Rev. Mus. La Plata, n.s., Paleont., **3**:265–308.

Risso Dominguez, Carlos. 1949. Estratigrafía de las barrancas de Chapadmalal y Vorohué. Estudios, **81**:353–372; 419–431.

Romer, Alfred Sherwood. 1966. Vertebrate Paleontology. 3rd ed. Chicago, Univ. Chicago Press.

Rusconi, Carlos. 1933. New Pliocene remains of diprotodont marsupials from Argentina. Jour. Mammal., **14**:244–250.

———. 1936. La supuesta afinidad de *Argyrolagus* con los Typotheria. Bol. Acad. Nac. Cien. Córdoba, **33**:173–182.

———. 1967. Animales extinguidos de Mendoza y de la Argentina. Mendoza, Edición Oficial.

Schlosser, Max. 1923. Mammalia. In: Grundzüge der Paläontologie (Paläozoologie), by Karl A. von Zittel, F. Broili, and M. Schlosser. 4th ed. Munich and Berlin, R. Oldenbourg.

Schmidt-Nielsen, Knut. 1964. Desert Animals. Physiological Problems of Heat and Water. Oxford, Clarendon Press.

Scott, William B. 1905. Insectivora. Repts. Princeton Exped. Patagonia, **5**:365–383.

———. 1913. A history of Land Mammals in the Western Hemisphere. New York, Macmillan.

———. 1937. Ibid. Revised ed. New York, Macmillan.

Simpson, George Gaylord. 1928. Affinities of the Polydolopidae. Amer. Mus. Novit., No. **323**:1–13.

———. 1932. The supposed occurrences of Mesozoic mammals in South America. Amer. Mus. Novit., No. **530**:1–9.

———. 1932. *Cochilius volvens* from the *Colpodon* beds of Patagonia. Amer. Mus. Novit., No. **557**:1–13.

———. 1933. The "plagiaulacoid" type of mammalian dentition. A study of convergence. Jour. Mammal., **14**:97–107.

———. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., **85**:i–xvi, 1–350.

———. 1948. The beginning of the Age of Mammals in South America. Bull. Amer. Mus. Nat. Hist., **91**:1–232.

Simpson, George Gaylord, José Luis Minoprio, and Bryan Patterson. 1962. The mammalian fauna of the Divisadero Largo Formation, Mendoza, Argentina. Bull. Mus. Comp. Zool., **127**:239–293.

Sinclair, William J. 1906. Palaeontology. Part III. Marsupialia of the Santa Cruz Beds. Repts. Princeton Univ. Exped. to Patagonia, 1896–1899, **4**, Part 3:333–460, Princeton and Stuttgart.

Stoll, N. R., *et al.* 1961, 1964. International Code of Zoological Nomenclature Adopted by the XV International Congress of Zoology. London, International Trust for Zoological Nomenclature.

Stromer, Ernest. 1932. *Palaeothentoides africanus* nov. gen., nov. spec., ein erstes Beuteltier aus Afrika. Sitzungsber. math.-nat. Abt. Bayer. Akad. Wiss., for 1931:177–190.

Thomas, Oldfield. 1895. On *Caenolestes*, a still existing survivor of the Epanorthidae of Ameghino, and the representative of a new

family of recent marsupials. Proc. Zool. Soc. London for 1895:870–878.

TROUESSART, EDOUARD LOUIS. 1898. Catalogus mammalium tam viventium quam fossilium. Nova editio (prima completa). Part 5. Berlin, Friedländer und Sohn.

WEBSTER, DOUGLAS B. 1961. The ear apparatus of the kangaroo rat, *Dipodomys*. Amer. Jour. Anat., **108**:123–148.

———. 1962. A function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys*. Physiol. Zool., **35**:248–255.

WOODWARD, ARTHUR SMITH. 1898. Outlines of Vertebrate Palaeontology for Students of Zoology. Cambridge, the University Press.

ADDENDUM

Since this study was sent to the editor several relevant publications and personal communications have been received. These importantly supplement the preceding text but do not require its substantial alteration. They are here discussed and references are given.

Distribution. Pascual *et al.* (1966, received in 1968) would modify the correlation and nomenclature of strata containing argyrolagids. They leave open the question whether the Chapadmalal Formation is later than the Monte Hermoso Formation or only of a different facies, but in any case maintain that the known mammalian faunas in those formations are not sufficiently distinct for recognition of different formal ages and stages. They therefore refer the Chapadmalal Formation to the Monte-Hermosan ("Montehermosense") stage, correlated with the early and middle Blancan of North America and considered late Pliocene as a whole. (Late Blancan is now generally considered Pleistocene; opinions differ as to whether any of the earlier Blancan should be referred to the Pliocene and if so, how much.)

Following a second thought by J. L. Kraglievich (1959), Pascual *et al.* (1966) now considered the Vorohué and San Andrés formations as inseparable and refer them (together) and a separate Barranca de los Lobos Formation to an Uquian ("Uquiense") stage, correlated with the late Blancan as early Pleistocene. As noted earlier in the present study, *Microtragulus* occurs in those formations and may be added to their faunal list. It also occurs in the Huayquerian ("Huayqueriense"), a preferable name for the Araucarian, but not in Buenos Aires Province, to which the work of Pascual *et al.* (1966) is confined.

For the most part, collectors used the formational terminology of J. L. Kraglievich (1952), which, whether accepted as definitive or not, does place the specimens in real and published rock sequences. It therefore still seems best to retain those distributional data, as I have in this publication. The exact placing of the Pliocene-Pleistocene boundary remains moot in South America and indeed everywhere else. The different placing of it by Pascual *et al.* (1966) does not significantly alter the indicated known span of the Argyrolagidae, from probable middle Pliocene to at least early and possibly middle Pleistocene.

Classification. Ringuelet (1966, received in 1968), in the same volume as Pascual *et al.* (1966), has redefined family and genus and figured a previously unpublished specimen. She considers Argyrolagidae Ameghino, 1904, a synonym of Microtragulidae Reig, 1958; *Argyrolagus* Ameghino, 1904, a synonym of *Microtragulus* Ameghino, 1904; and *M. argentinus* Ameghino, 1904, a synonym of *A. palmeri* Ameghino, 1904. Reasons for not accepting those synonymies have been adequately discussed here on previous pages. Ringuelet's family definition is valid for the taxon I call Argyrolagidae, except for the subsequent discovery that metatarsals III and IV are not in fact fused. Her generic definition, as regards mandible and dentition, is essentially a summary description of the previously undescribed specimen, figured by her in plate X, figs. I and J. It is in that respect a useful supplement but of course does not apply to the specimens, species, and genera of the whole family. The description, original in Spanish, may be translated as follows:

"Mandibular ramus short and high, flat internally, lightly convex externally, with lower border very convex; anterior border of the masseteric crest strongly marked. Dental formula $\overline{2.0.1.4.}$ I_1 large, compressed, hypsodont, reniform in section, convex externally and concave internally, implanted anteroposteriorly in the same line as the molariform series, so that the incisive border is very narrow, intra-alveolar part near the lower border parallel to the midline of the symphysis. I_2 approximately ovoid in section, with the internal face somewhat flatter, size similar to I_1. P_3 (?) separated from I_2 by a diastema approximately a little less than the diameter of the two incisors, small, triangular in section, approximately isosceles with the base posterior, with rounded angles, implanted obliquely postero-externally. Molars octodontiform, with peripheral cusps of doubtful homologies, the coat of enamel becoming thin and almost disappearing on the anterior fold and on the inner side of the posterior face. M_{1-3} subequal, with the anterior lobe (trigonid) larger than the posterior (talonid), triangular in section, with approximately equal sides; posterior lobe compressed anteroposteriorly. M_4 smaller, with the posterior lobe narrower than the anterior but less compressed anteroposteriorly than on the other molars. M_{1-2} somewhat imbricated, with the anterior somewhat displaced externally."

Dr. Rosendo Pascual (personal communication, 25 February 1969) has kindly added the information that this specimen is in the Museo de la Plata and was collected in 1961 in the Chapadmalal-Miramar region in the cliffs of the Playa de las Palomas, a little north of the Balneario Chapadmalal, in beds designated by J. L. Kraglievich (1952) as belonging to the Chapadmalal Formation. Pascual adds the following measurements and descriptive notes (here translated):

"Height of mandibular ramus on the external face below the first cheek tooth. . . . 4.3 mm.

Table 3. Relative Lengths of Some Pelvic Dimensions in Certain Marsupials and Rodents.

A. Postacetabular (to the ischial spine) length as a percentage of preacetabular (iliac) length.

B. Length from center of acetabulum to center of sacral attachment as a percentage of length from center of sacral attachment to anterior end of ilium.

Figures are from single specimens and may vary considerably in the species and genera.

Species	A	B
Argyrolagus scagliai	54	88
Caenolestes obscurus	51	206
Dipodomys merriami	62	117
Allactaga mongolica	81	109

Supplement to Table 3
(Ratio B not taken)

	A
Antechinomys spenceri, single male skeleton	59
Notomys mitchelli, four skeletons.	Range 52–56 Mean 53.5

"Height of manibular ramus on the external face below the third cheek tooth. . . . 5.3 mm.

"Length of distance from anterior face of the first incisor to the last cheek tooth along the alveolar border. . . . 11.8 mm.

"Length of space occupied by the cheek teeth along the alveolar border. . . . 7.8 mm.

"The anterior incisor extends within the alveolus to beneath the third cheek tooth (its open base is visible). The symphyseal surface extends to beneath the anterior face of the second cheek tooth (the first of those bilobate). Posterior to the last cheek tooth two small foramina can be discerned, one behind the other, which might possibly belong to a very small shed molar. However, the posterior expansion of the talonid of the last cheek tooth preserved makes me think that there was no additional molar. The masseteric crest projects very strongly and stops abruptly at mid-height

of the mandibular ramus, below the posterior lobe of the penultimate molar present."

This specimen belongs to the genus to which the name *Argyrolagus* is somewhat arbitrarily applied in the present study. Specific reference is doubtful on the data available, but should be possible with further study of the original. Dr. Pascual has kindly arranged for such study, but it has been decided not to delay the present publication for that purpose.

Affinities. Dr. John Kirsch (1968) has now published a summary of his new classification of marsupials, based largely but not exclusively on serological evidence. In still more succinct form, his arrangement is as follows:

Superorder Marsupialia
  Order Polyprotodonta
    Suborder Didelphimorphia
      Superfamily Didelphoidea
      Superfamily Borhyaenoidea
    Suborder Dasyuromorphia
      Superfamily Dasyuroidea
    Suborder Paramelemorphia
      Superfamily Perameloidea
  Order Paucituberculata
      Superfamily Caenolestoidea
  Order Diprotodonta
      Superfamily Vombatoidea
      Superfamily Phalangeroidea
      Superfamily Tarsipedoidea

This represents a truly important contribution, especially as regards affinities within his Diprotodonta (details not given here), but it would only impede any placing of the Argyrolagidae, not listed by Kirsch. I do not see how they could reasonably be put in any of his orders, still less reasonably in any lower taxon. The alternative within that framework would be to erect still another order for the argyrolags alone. That seems to me unjustified on balance and at present, and I hope that it does not tempt any nomenclator. I still feel that for overall use, including extinct groups, it is impractical or undesirable to try to establish taxa of categorical rank between superfamilies and Marsupialia even though a reasonable case on the basis of living forms has been made (by Ride as well as Kirsch) for subdivision into several orders.

Kirsch's inclusion of Perameloidea in Polyprotodonta is also, but less essentially, relevant to the present study. It is based on his finding closer serological resemblances between Perameloidea and Dasyuroidea than between either and Phalangeroidea. If that is a reliable *phylogenetic* indicator, then we must conclude that typical and complete syndactyly, contrary to my conclusion in the body of this paper, has in fact arisen quite independently twice among the Marsupialia. In support of this possibility, Kirsch has also pointed out (in personal communication) that incipient syndactyly was long ago reported in the Didelphidae.[54] He kindly sent me a photograph of the hind foot of *Caluromys derbianus* to illustrate this tendency. The photograph shows digits II and III nearly (not quite) equal and less divergent than the other digits, but apparently without

[54] Bensley (1903) said of *Marmosa* that "there is here, in some species, an indication of the syndactylous condition of the Phalangeridae," and that the conditions in *Marmosa* "are repeated in *Caluromys*." His figure of the pes of *Marmosa priscilla* (pl. 7, fig. 7) is almost exactly like that of *Dromicia nana* (pl. 7, fig. 13), and the latter was in fact probably another specimen of *M. priscilla*. In both, digits II and III are subequal and appressed, but they do not appear syndactylous and they are very unlike any phalangerid. In his diagnosis of *Marmosa*, Tate (1933) included, "Almost no trace of syndactyly." That implies that there is *some* trace. Being given as diagnostic, it might also imply that a more definite trace occurs in some allied genus, but I do not find a statement to that effect in Tate's work. Another paper (Tate, 1939) in which he explicitly discussed both *Marmosa* and *Caluromys* says nothing about syndactyly in either one. It is perhaps not surprising that little attention has hitherto been paid to these hints of incipient syndactyly in didelphids.

TABLE 4. LENGTHS (IN MILLIMETERS) AND PROPORTIONS OF LIMB BONES IN AN ARGYROLAGID, SOME MARSUPIALS, AND SOME RODENTS (EXCEPT AS INDICATED BELOW, ALL MEASUREMENTS ON SINGLE ADULT SPECIMENS).

Taxa	A Humerus	B Radius	C Femur	D Tibia	E Metatarsus	A/B	C/D	D/E	A/C	(A+B)/(C+D)
Argyrolagidae:										
Argyrolagus scagliai	ca. 17½	ca. 18½	43.9	60.4	35.6	ca. .94	.73	1.69	ca. .40	ca. .35
Caenolestidae:										
Caenolestes obscurus	13.9	15.0	14.3	22.3	8.6	.93	.64	2.59	.97	.79
Rhyncholestes raphanurus	14.0	15.5	15.3	22.6	8.6	.90	.68	2.63	.91	.79
Dasyuridae:										
*Antechinomys spenceri**	13.8	20.9	20.8	29.0	15.3	.66	.72	1.90	.66	.78
Macropidae:										
Bettongia lesueuri	34	42	81	114	40	.81	.71	2.85	.42	.39
Petrogale penicillata	70	87	147	187	58	.80	.79	3.22	.48	.47
Heteromyidae:										
Dipodomys merriami	11.7	14.9	23.9	34.3	17.0	.78	.70	2.03	.49	.46
Dipodidae:										
Allactaga mongolica	14.3	17.7	34.1	49.8	32.5	.81	.68	1.53	.42	.38
Jaculus sp.	15.7	–	39.5	58.3	40.0	–	.68	1.46	.40	–

* Data for this species are means for seven preserved (not skeletonized) specimens measured on X-ray films. Even as means, these cannot be as accurate as direct measurements on bones, but they are believed to suffice for present comparative purposes. The specimens belong to the Western Australian Museum. The radiographs were taken by Basil Marlow at the Australian Museum at the instance of W.D.L. Ride especially for the present study.

SUPPLEMENT TO TABLE 4

	A	B	C	D	E	A/B	C/D	D/E	A/C	(A+B)/(C+D)
Antechinomys spenceri, single male skeleton	16.8	24.8	22.8	34.6	6.19	.64	.66	1.82	.74	.72
Notomys mitchelli, single female skeleton	14.7	17.3	25.5	35.7	17.9	.85	.71	2.00	.58	.50

common integument beyond the metatarsals. This is not clear or developed syndactyly, even though it could well represent a primitive basis for evolution of syndactyly. There is also the fact, well known but overlooked by me when I wrote earlier parts of this study, that the placental *Potamogale* has advanced syndactyly (see e.g., Walker *et al.*, 1968, figure on p. 118) closely similar to that of the Phalangeroidea and certainly of completely independent origin. Since that condition has arisen in two groups by pure convergence, it could have arisen two or more times by parallelism within the Marsupialia.

The question of possible independent

origin of syndactyly in Perameloidea and Phalangeroidea must thus still be considered open, but this does not particularly weaken my previous conclusions that the Argyrolagidae were not derived from or specially related to either group. First, all known members of both those groups are indeed syndactylous, and it seems quite certain that no ancestor of the Argyrolagidae ever was, even to an incipient degree. Second, evidence against such relationships is supported by this point, but includes so much else as to be reasonably conclusive even without it.

Biology. Since this paper was written, a visit to the National Museum of Victoria, Melbourne, Australia, permitted me to make measurements on a skeleton of *Antechinomys spenceri*, more reliable than the x-ray data in Table 4, and to add homologous data for *Notomys mitchelli*. At La Trobe University, near Melbourne, live specimens of both species were observed through the kindness of Miss Meredith Stanley. *N. mitchelli*, like most *Dipodomys*, has a slow quadrupedal walk, a fast bipedal walk, a bipedal ricochet, and a startle reaction straight up.

In the following supplements, measurements are as in the previous tables under the same alphabetical designations.

It is confirmed that *Antechinomys* has a relatively longer forelimb than in the definitely bipedal forms and that its radius is peculiarly long relative to its humerus. The limb proportions of *Notomys* are close to those of *Dipodomys*, and these two only distantly related rodents are remarkably similar in appearance, habits, and anatomy throughout. Either one probably gives a fair idea of what *Argyrolagus* was like when alive, even though they are placentals and it was a marsupial.

REFERENCES IN THE ADDENDUM

BENSLEY, B. A. 1903. On the evolution of the Australian marsupials, with remarks on the relationships of the marsupials in general. Trans. Linn. Soc. London, 2nd ser., Zool., **9**:83–217.

KIRSCH, J. A. W. 1968. Prodromus of the comparative serology of Marsupialia. Nature, **217**:418–420.

KRAGLIEVICH, J. L. 1959. Contribución al conocimiento de la geología cuartaria en la Argentina. Com. Mus. Argentino Cien. Nat., **1**, no. 17:1–9.

PASCUAL, R., E. J. ORTEGA HINJOSA, D. GONDAR, AND E. TONNI. 1966. Les edades del Cenozóico mamalifero de la Provincia de Buenos Aires. *In:* A. V. Borrello, ed., Paleontografia Bonaerense. Comis. Invest. Cien., Prov. Buenos Aires, La Plata, fascículo IV:3–27.

RINGUELET, A. B. DE. 1966. Marsupialia. *In*: A. V. Borrello, ed., Paleontografia Bonaerense, Comis. Invest. Cien., Prov. Buenos Aires, La Plata, fascículo IV:46–59.

TATE, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*. Bull. Amer. Mus. Nat. Hist., **66**:1–250.

———. 1939. The mammals of the Guiana Region. Bull. Amer. Mus. Nat. Hist., **76**:151–229.

WALKER, E. P., F. WARNICK, S. E. HAMLET, K. I. LANGE, M. A. DAVIS, H. E. VIBLE, AND P. F. WRIGHT. 1968. Mammals of the World. 2nd ed., revised by J. L. Paradiso. 2 volumes. Baltimore, Johns Hopkins Press.

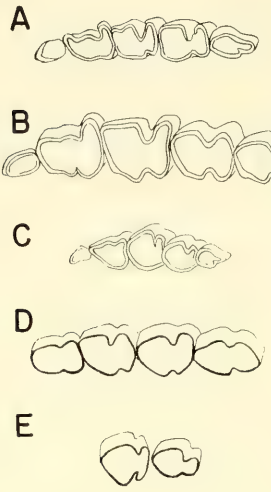


Figure 1. Crown views of right lower cheek teeth of Argyrolagidae. A, *Microtragulus reigi*, MMMP No. 960-M, P_3-M_4. B, *Argyrolagus scagliai*, MMMP No. 741-M, P_3-M_4. C, *Microtragulus catamarcensis*, MACN No. 5529, P_3-M_4. D, *Argyrolagus palmeri*, type, M_{1-4}, after Kraglievich (1931), reversed from left side. E, ?*Argyrolagus parodii*, type, M_{3-4}, M_3 after Rusconi (1936) and M_4 after Rusconi (1933), both reversed from left side. All × 4.

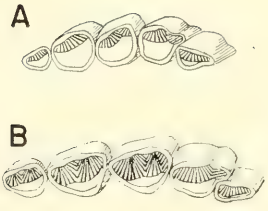


Figure 2. Crown views of right P^3-M^4 of Argyrolagidae. A, *Microtragulus reigi*, MMMP No. 661-S. B. *Argyrolagus scagliai*, MMMP No. 785-S. Both × 4.

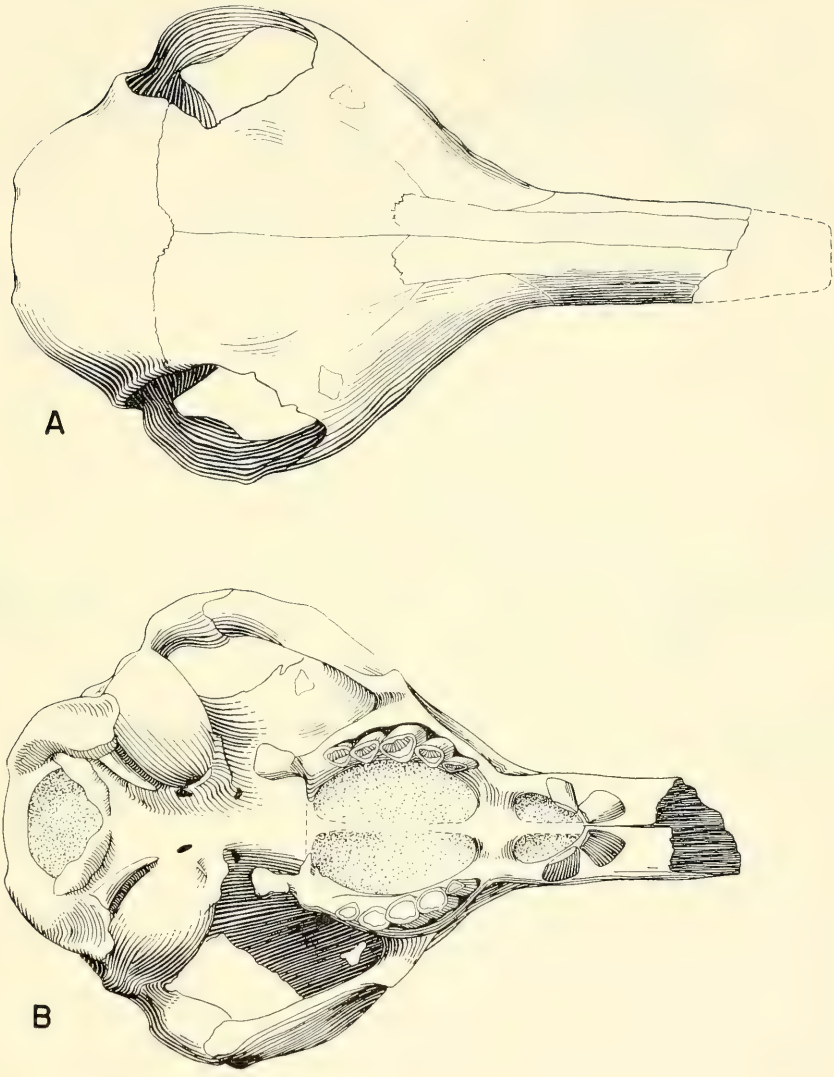


Figure 3. *Argyrolagus scagliai*, MMMP No. 785-S, skull. A, Dorsal view. B, Ventral view. In this and the following figures of the skeleton of this individual, some restoration has been made by reversing to one side parts present on the other side and some distortion has been modified. Both × 2.

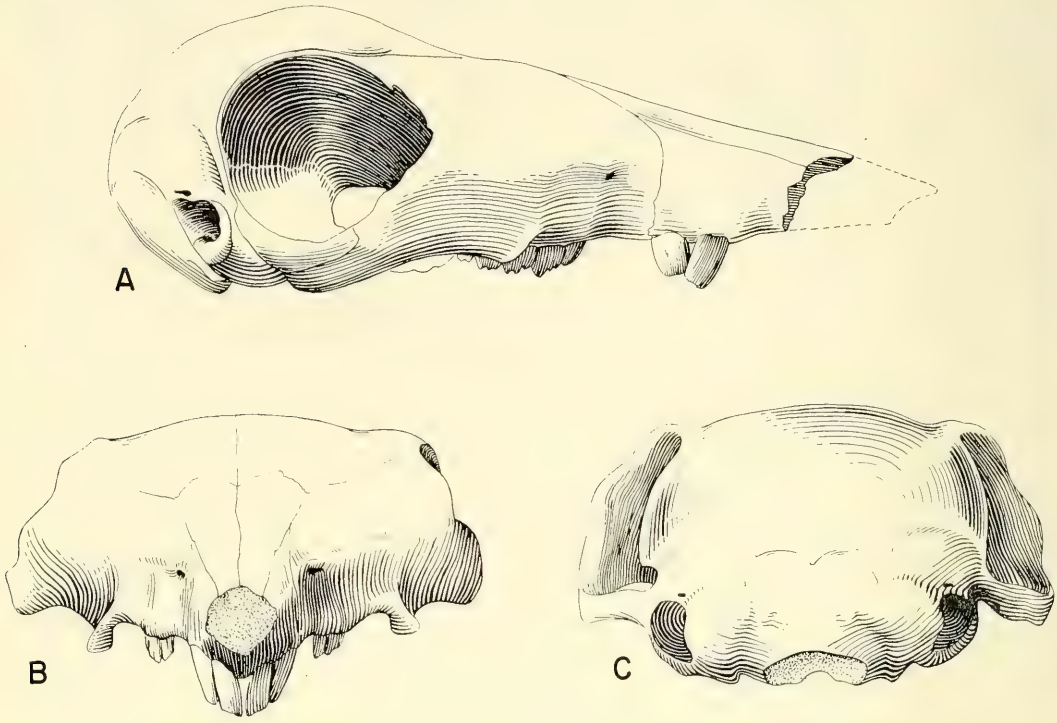


Figure 4. *Argyrolagus scagliai*, MMMP No. 785-S, skull. A, Right lateral view. B, Anterior view. C, Posterior view. Snout in broken outline in A is hypothetical but suggested by known part in *Microtragulus reigi*. In B the broken snout has not been restored. All × 2.

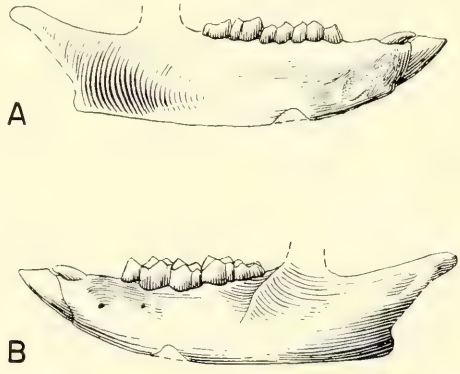


Figure 5. *Argyrolagus scagliai*, MMMP No. 785-S, left ramus of mandible. A, Medial or lingual view. B, Lateral or labial view. The posterior part of this specimen is distorted by breakage and has been reconstructed with reference to occlusion with upper teeth of the same individual and placing of the condyle of the lower jaw on the glenoid surface of the skull. Both × 2.

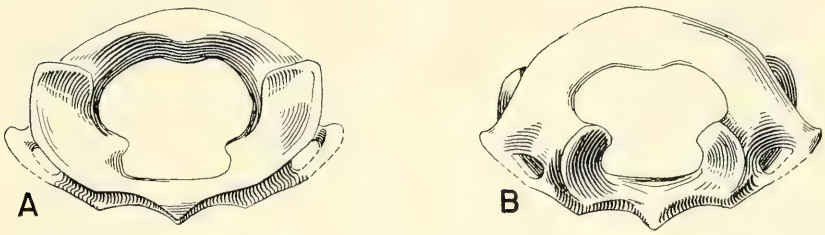


Figure 6. *Argyrolagus scagliai*, MMMP No. 785-S, atlas. A, Anterior view. B, Posterior view. Both × 4.

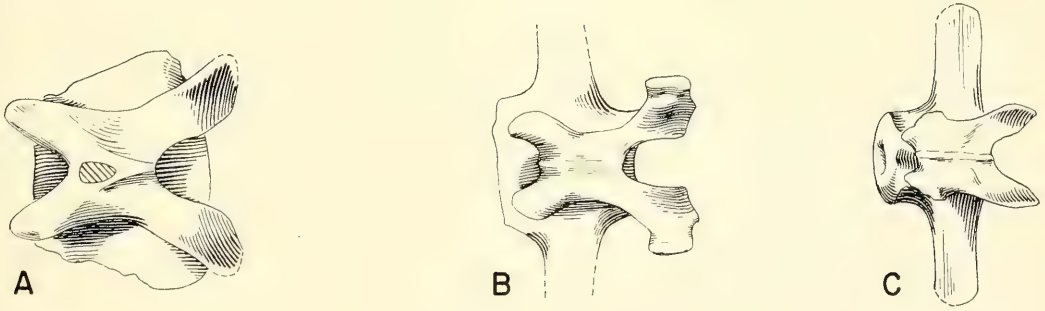


Figure 7. Dorsal view of anterior caudal vertebrae of Argyrolagidae. A, B, *Argyrolagus scagliai*, MMMP No. 785-S. C, Vertebra preserved with and possibly belonging to MACN No. 7130, type of *Microtragulus argentinus*. All × 4.

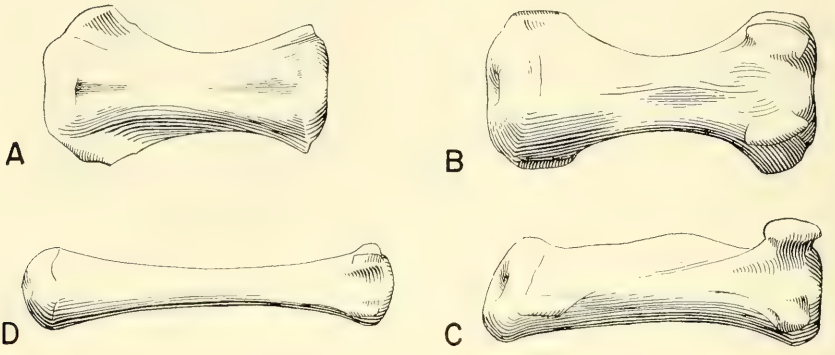


Figure 8. *Argyrolagus scagliai*, MMMP No. 785-S, medial to posterior caudals. A, Relatively anterior, probably first after kind of vertebrae shown in Fig. 7A, B, ventral view. B, More posterior vertebra, dorsal view. C, Same as B, right lateral view. D, Still more posterior vertebra, right lateral view. All × 4.

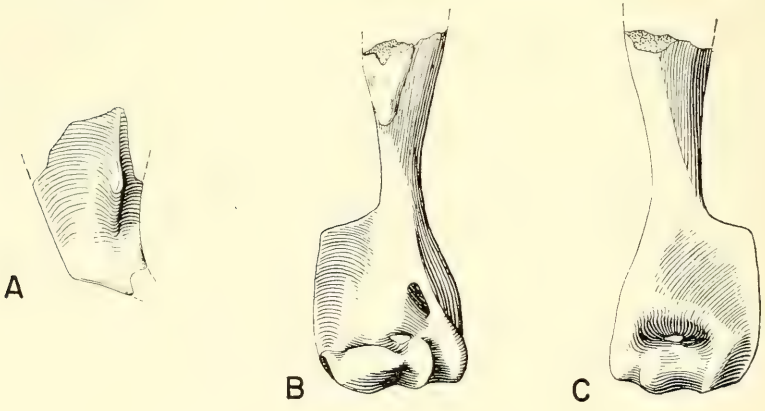


Figure 9. *Argyrolagus scagliai*, MMMP No. 785-S. A, Fragment of lower end of right scapula, lateral view. B, Right humerus lacking proximal end, anterior view. C, Same as B, posterior view. All × 3.

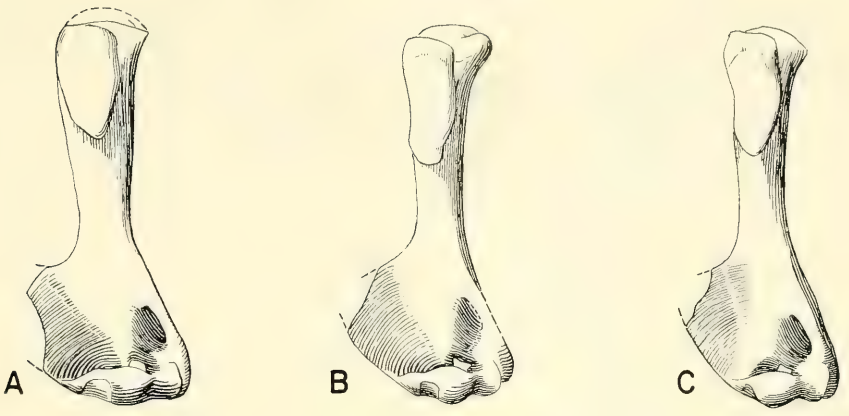


Figure 10. Anterior views of right humeri of Argyrolagidae. A. MMMP No. 795-S. B, MMMP No. 396-M. C, MMMP No. 395-M. For possible identifications see text. All × 3.

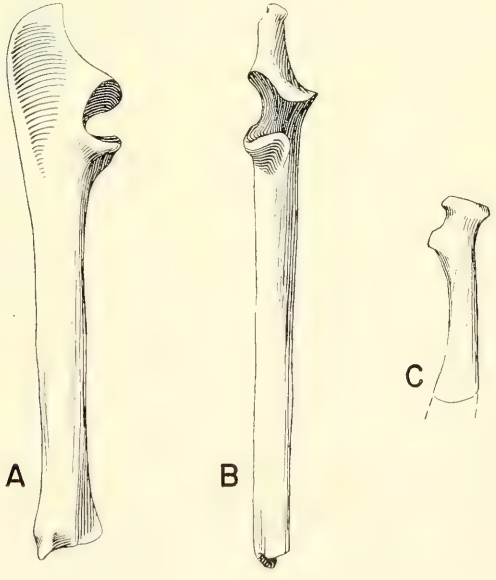


Figure 11. *Argyrolagus scagliai*, MMMP No. 785-S. A, Right ulna, lateral view. B, Same as A, anterior view. C, Proximal end of right radius, anterior view. All × 3.

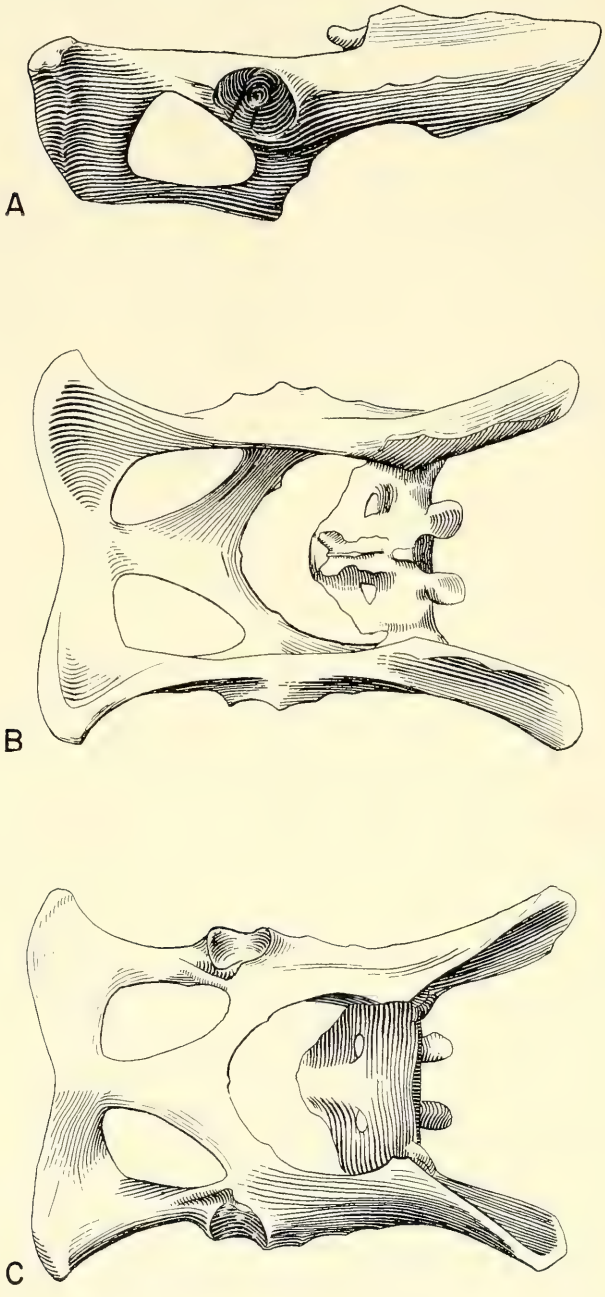


Figure 12. *Argyrolagus scagliai*, MMMP No. 785-S, sacrum and pelvis. A, Right lateral view. B, Dorsal view. C, Ventral view. All × 2.

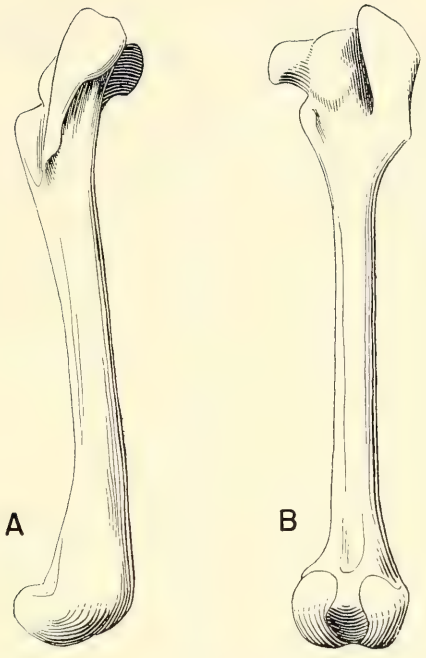


Figure 13. *Argyrolagus scagliai*, MMMP No. 785-S, right femur. A, Lateral view. B, Posterior view. Both × 2.

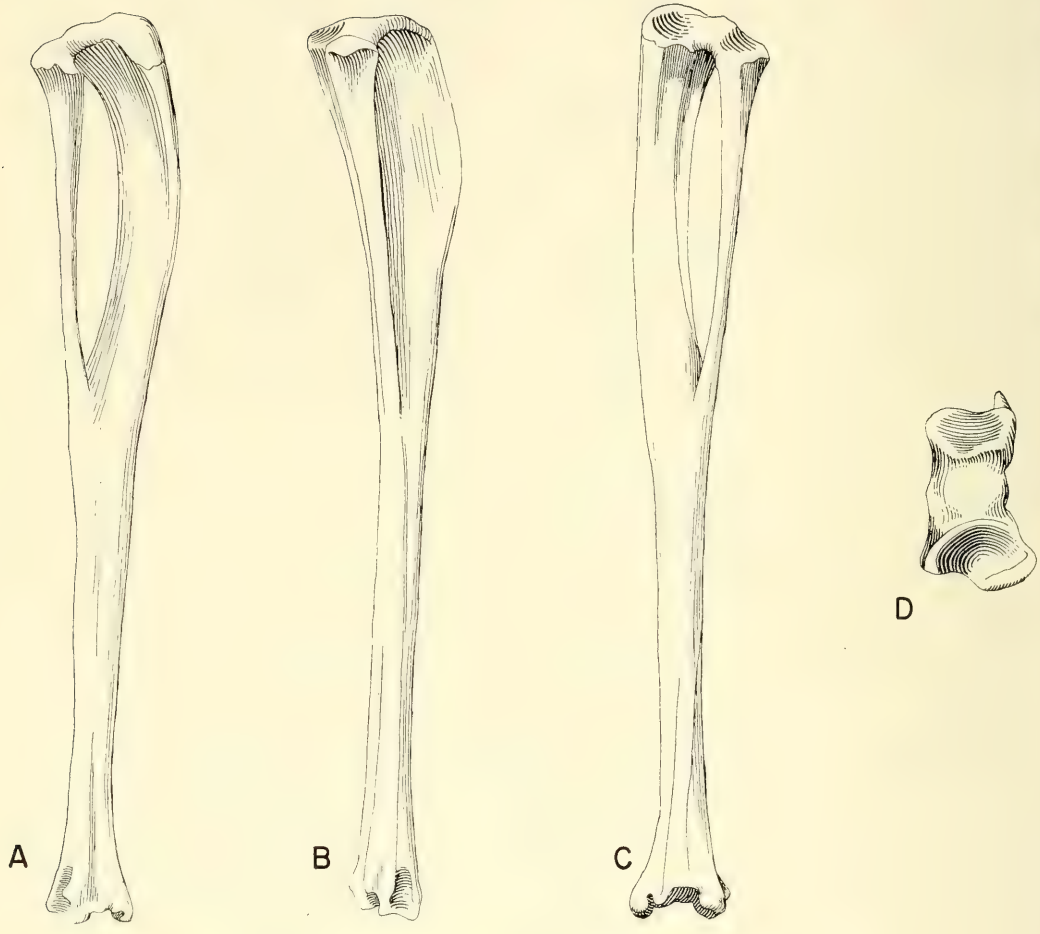


Figure 14. *Argyrolagus scagliai*, MMMP No. 785-S, right tibio-fibula. A, Anterior view. B, Lateral view. C, Posterior view. D, Distal view. A, B, C × 2. D × 4.

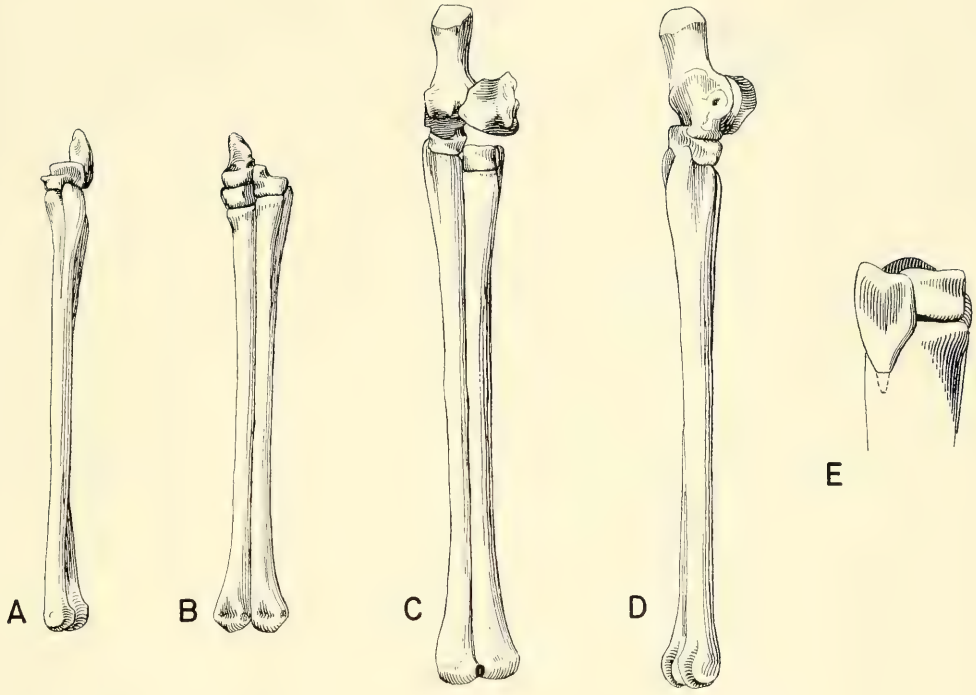


Figure 15. Tarsals and metatarsals of Argyrolagidae. A, *Microtragulus argentinus*, MACN No. 7130, left scaphoid, ectocuneiform, cuboid, and metatarsals III–IV, lateral view. B, Same as A, anterior (or dorsal) view. C, *Argyrolagus scagliai*, MMMP No. 785-S, right calcaneum, astragalus, cuboid, ectocuneiform, and metatarsals III–IV, anterior (or dorsal) view. D, Same as C, lateral view. E, Same individual as C–D, medial view of vestige of metatarsal II, ectocuneiform, and proximal end of metatarsal III. A–D × 2. E × 4.

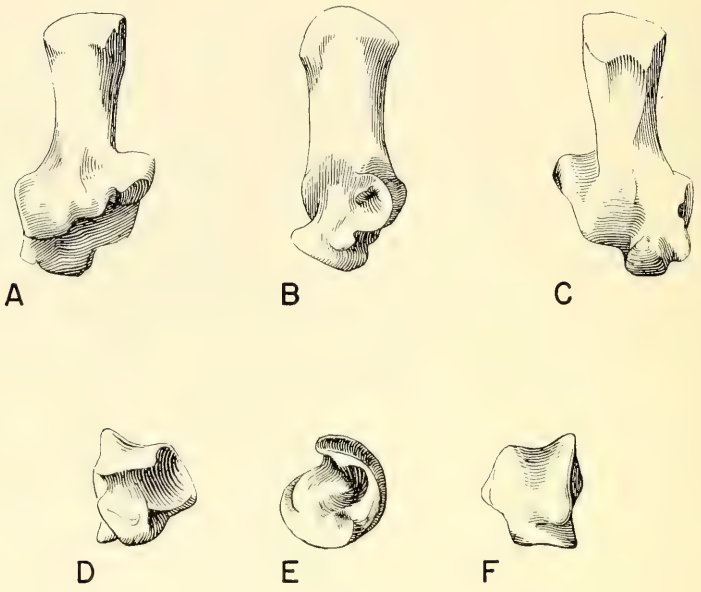


Figure 16. *Argyrolagus scagliai*, MMMP No. 785-S. A, Right calcaneum, dorsal view. B, Same as A, lateral view. C, Same as A, ventral view. D, Right astragalus, ventral view. E, Same as D, lateral view. F, Same as D, dorsal view. All × 4.

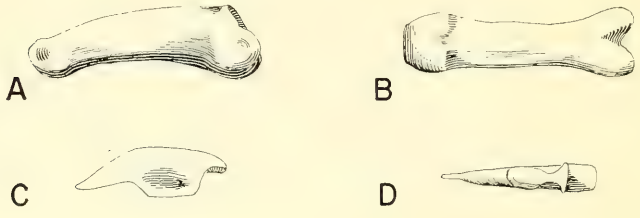
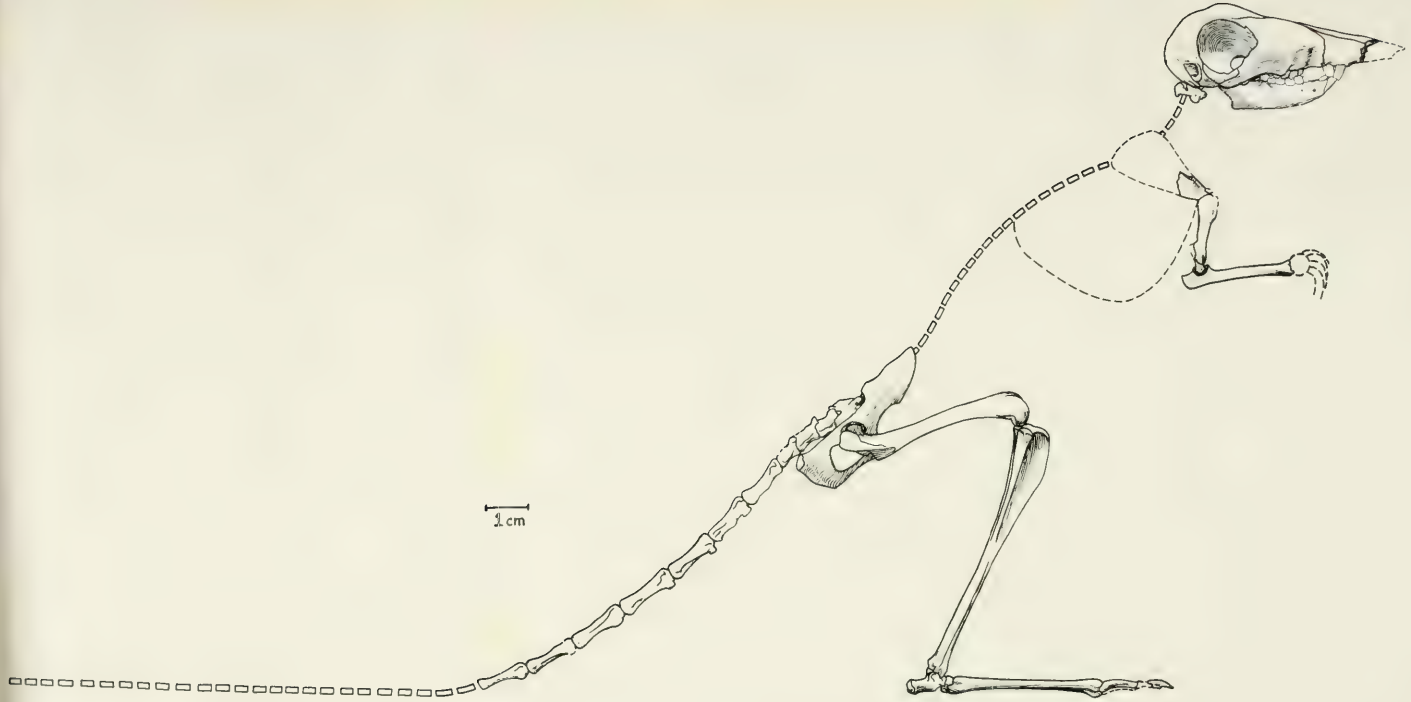


Figure 17. *Argyrolagus scagliai*, MMMP No. 785-S. A, Proximal phalanx, medial view. B, Same as A, ventral view. C, Distal phalanx, medial view. D, Same as C, ventral view. All × 4.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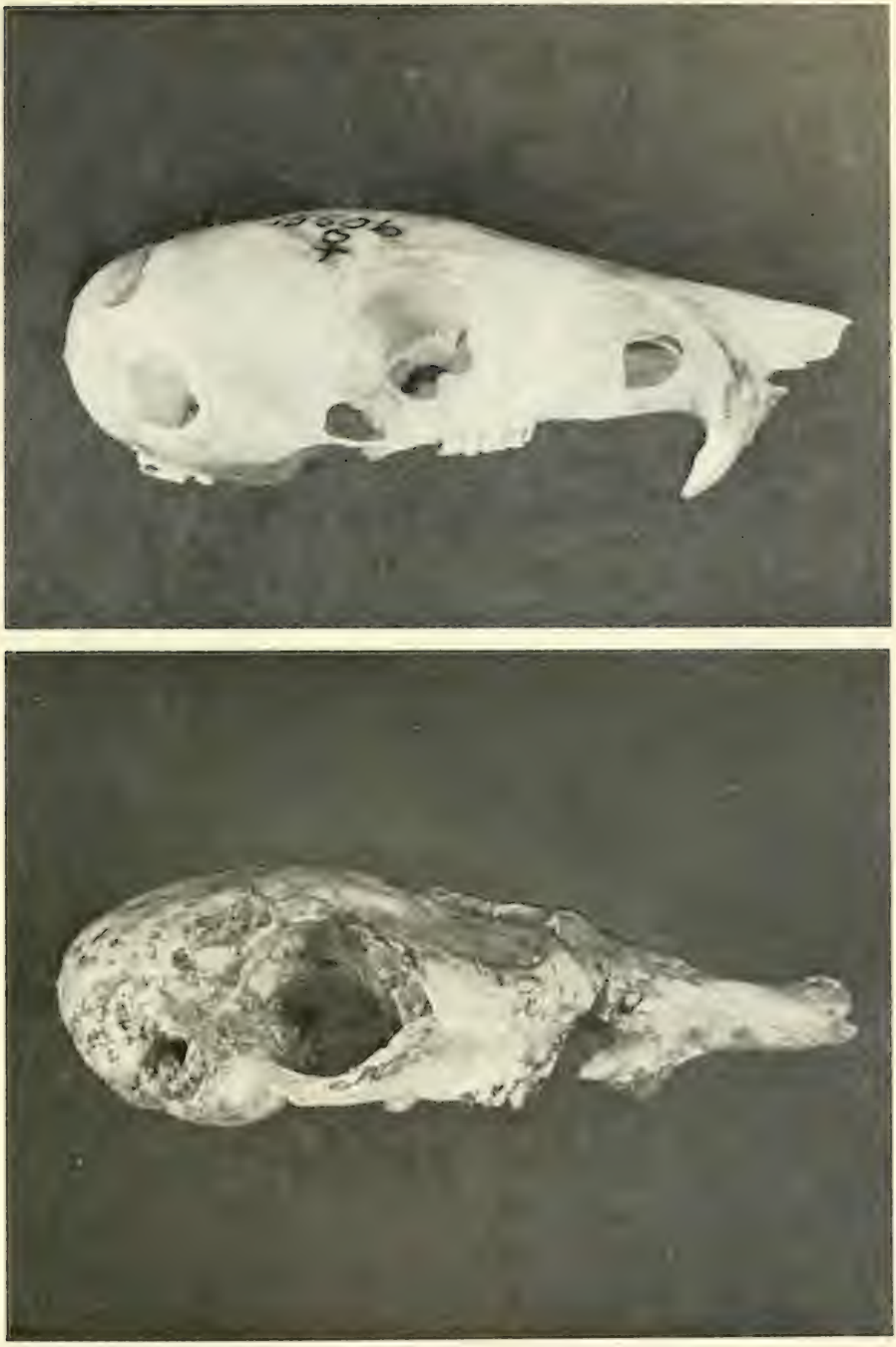

Plate 1. Above. *Dipodomys merriami*. University of Arizona, Zoology No. 15506. Skull. Right lateral view. Ca. × 2. Below. *Microtragulus reigi*. MMMP No. 691-S. Skull. Right lateral view. Slightly less than × 2½. This and the following two plates illustrate the extraordinary adaptive similarity in these two groups, which evolved from entirely different ancestors.

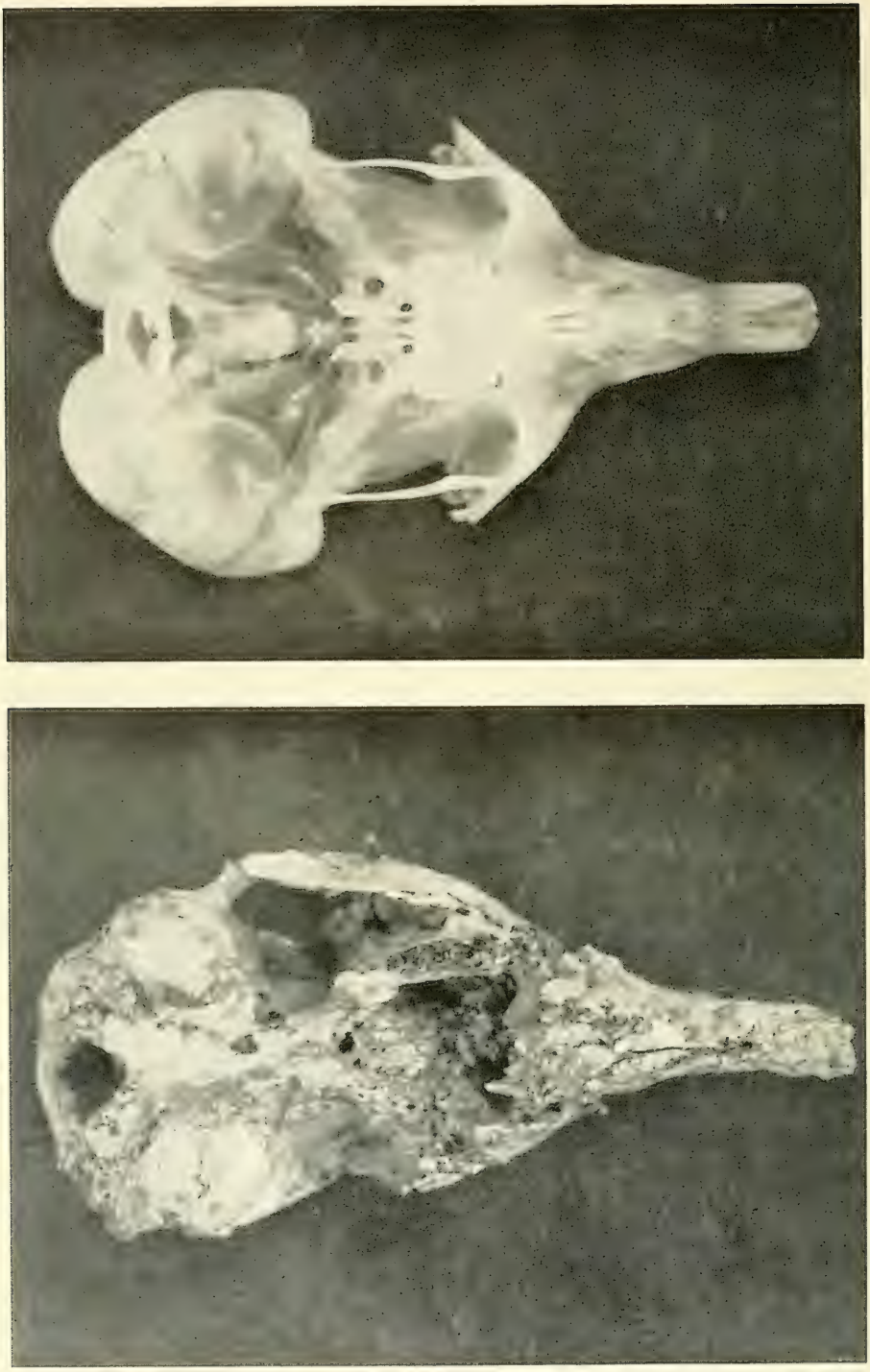

Plate 2. Same specimens and enlargements as Plate 1. Ventral views.

Plate 3. Same specimens and enlargements as Plate 1. Dorsal views.

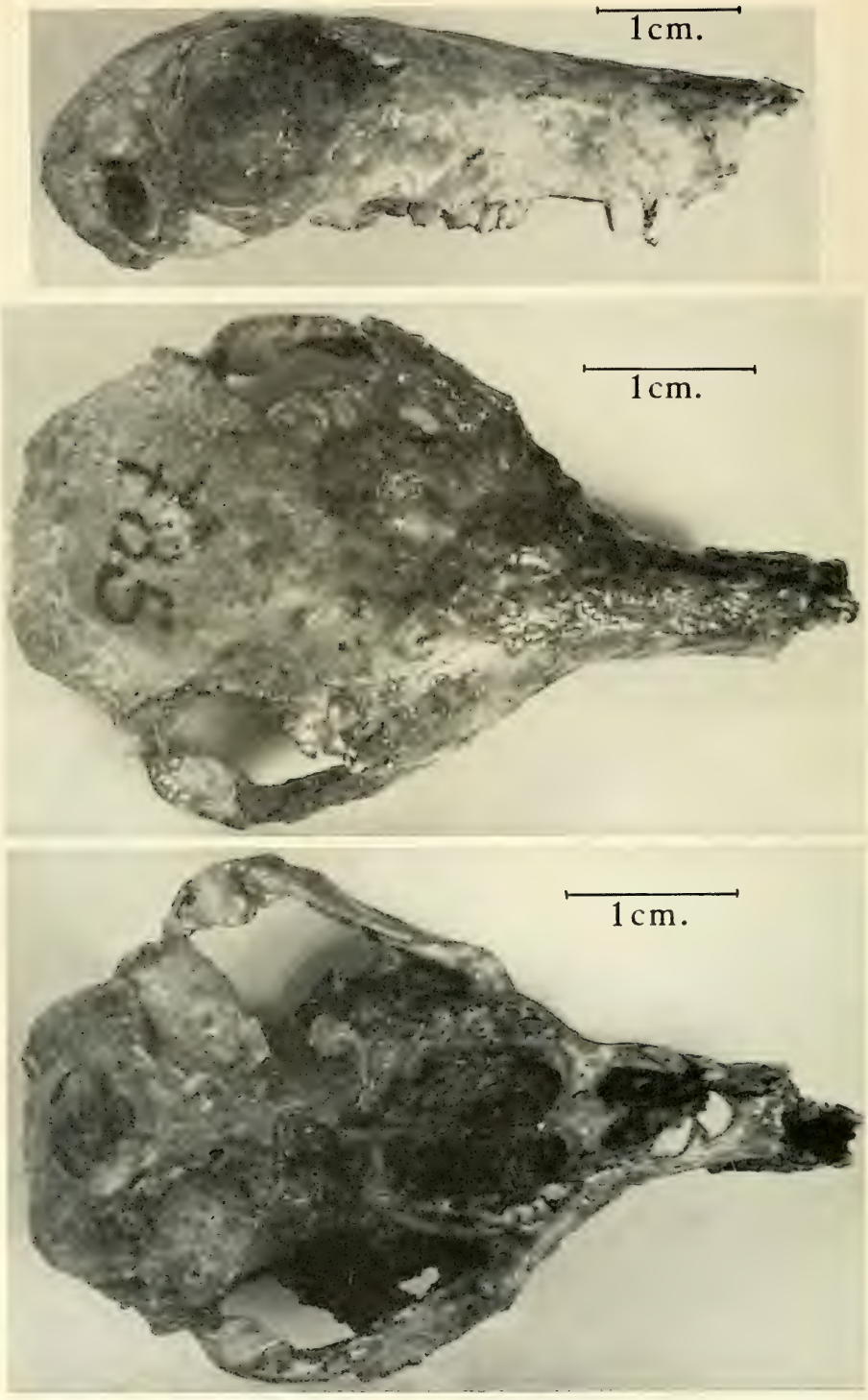

Plate 4. *Argyrolagus scagliai*. MMMP No. 785-S. Skull. Right lateral, dorsal, and palatal views. Photographs supplied by Dr. O. Reig.

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North American Fossil Anguid Lizards

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NORTH AMERICAN FOSSIL ANGUID LIZARDS

CHARLES A. M. MESZOELY[1]

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ABSTRACT

A survey of osteological and epidermal scalation characters of extant anguid lizards indicates that the Recent species fall into three groups worthy of subfamily status: (1) Gerrhonotinae (including *Gerrhonotus, Abronia,* and possibly *Coloptychon*), (2) Anguinae (including *Ophisaurus* and *Anguis*), (3) Diploglossinae (including *Diploglossus, Wetmorena,* and *Ophiodes*). Many characters were examined during this study, but the morphology of the frontal bones and body osteoscutes, presence or absence of a premaxillary foramen, and the participation of the postorbital in orbit formation are characters that have proved the most useful in both fossil and Recent forms.

Anguis is very close to *Ophisaurus,* differing from it only in features judged here to be degenerate. The ophisaurs are intermediate in many features between the Diploglossinae and the Gerrhonotinae, sharing with the former the unique premaxillary foramen and divided frontals, and with the latter a similar body scutellation. The anguines appear to be primitive in having toothed palatines and, in some species, toothed vomers.

Fossil remains unquestionably those of an anguid lizard first occur in late Cretaceous sediments of Wyoming and Montana. This anguid was first described by Gilmore (1928) as *Peltosaurus? piger* on the basis of two jaw elements. The generic assignment of this lizard was based on its having a tooth structure similar to that of the Oligocene *Peltosaurus granulosus.* A large number of previously unknown cranial elements recovered recently from the late Cretaceous Hell Creek Formation in Montana and from late Paleocene Bison Basin sediments in Wyoming indicates that this

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early anguid lizard is referable to *Pancelosaurus*, n. gen., rather than to *Peltosaurus*. *Pancelosaurus piger* exhibits a mosaic of characters in its known skeletal parts and shows resemblance to the Recent anguids *Ophisaurus*, *Gerrhonotus*, and *Diploglossus*. Since the body osteoscutes of the Cretaceous form most closely resemble those of *Gerrhonotus* and *Ophisaurus*, perhaps the extinct genus was already specialized toward the line leading to the latter two Recent genera. *Pancelosaurus piger* exhibits many of the same primitive and intermediate characters between the diploglossines and the gerrhonotines as do the ophisaurs, and it is regarded here as a primitive limbed member of the Anguinae. *P. piger* is known from the late Cretaceous through the late Paleocene and the genus extends into the middle Oligocene as *P. pawneensis* (formerly *Xestops pawneensis*).

The large Eocene and Oligocene fossil forms *Xestops*, *Peltosaurus*, *Melanosaurus*, *Glyptosaurus*, and *Arpadosaurus gazinorum*, n. gen., n. sp., may also have been derived from *Pancelosaurus* or its relatives, as indicated by a similar type of body osteoscute. These are more robust than those of *P. piger*, are always covered with tubercular mounds, and are often laterally sutured. This sculpture type is found only in the above forms, and in combination with a characteristic pattern of labial suturing between dentary and postdentary bones, indicates the distinctiveness of this group, which is placed here in a subfamily Glyptosaurinae. In this concept of the glyptosaurines, the Eocene species *Xestops vagans* appears to be the most primitive form and shares some primitive features of the frontal bones with *P. piger* while exhibiting the above-mentioned glyptosaurine characters. *Dimetopisaurus wyomingensis* Hecht is a synonym of *Xestops vagans*. *Arpadosaurus* appears to be also referable to the Glyptosaurinae as constituted here, and is structurally intermediate between *Melanosaurus* and *Glyptosaurus*. It is postulated that *Glyptosaurus* may have originated from a form like *Melanosaurus* through *Arpadosaurus*, but more evidence is needed to confirm this hypothesis, which is based on contemporaneous fossil genera. The glyptosaurines represent a side line of anguid evolution rather than being ancestors of the modern forms.

INTRODUCTION

Until recently, detailed anatomical knowledge of the cranium of fossil anguids was based only on Eocene and Oligocene forms. Most of this descriptive anatomical work was carried out by Gilmore (1928, pp. 91–144; 1938, pp. 16–21). The presence of anguid remains in earlier deposits (Upper Cretaceous and Paleocene) was indicated by Gilmore (1928, pp. 136–138), and later by Gazin (1956, p. 12) and Estes (1964, pp. 119–125). The latter author gave a detailed description of the maxilla and dentary of this early anguid, but it was not until recently that most of the cranial elements of this form were identified among thousands of fragmentary bones of other species from late Cretaceous Hell Creek Formation sites near Fort Peck Reservoir, McCone Co., Montana (Sloan and Van Valen, 1965). This large amount of fossil matrix was obtained through the method of screening and washing as described by McKenna (1962) and sorted for faunal studies now in progress by Estes, Berberian, and Meszoely (1969) (studies similar to that of Estes, 1964). These new finds not only gave us a more detailed knowledge of the cranial anatomy of this earliest known anguid, but also yielded information about the epidermal scalation.

In an attempt to shed new light on the evolution and interrelationships of the fossil and recent members of the Anguidae, the earliest well-known anguid, "*Peltosaurus*" *piger*, is described here in detail and its cranial elements are compared with those of Recent and fossil forms. It is referred below to *Pancelosaurus*, n. gen. Well over one hundred Recent skeletons, hundreds of fragmentary remains of *P. piger*,

and a great number of other fossil specimens, including the holotypes of most North American anguid species, have been examined. This study has resulted in reclassification of both modern and extinct anguids and has provided information on several phyletic lines within the Anguidae.

I wish to thank Richard Estes, Ernest E. Williams, Bryan Patterson, and Allen E. Greer for suggestions and criticism, and my wife, Janice Meszoely, for aid in collecting specimens.

I am also grateful to Craig C. Black, Carnegie Museum; James A. Hopson, then of the Peabody Museum, Yale University; Nicholas Hotton III, U. S. National Museum, and Robert E. Sloan, University of Minnesota, for the loan of specimens.

The illustrations were prepared by Miss Tehrie Holden (Figs. 7–9, 10d, 11–16) and Laszlo Meszoly (1–6, 17), the photographs by Fred Maynard.

This work was supported in part by NSF Grant GB-4303 to Richard Estes.

Abbreviations used here are as follows:

AMNH	American Museum of Natural History, New York, N. Y.
BM(NH)	British Museum (Natural History), London, England
CM	Carnegie Museum, Pittsburgh, Pa.
FAM	Frick collection at the American Museum of Natural History, New York, N. Y.
FMNH	Field Museum of Natural History, Chicago, Ill.
KU	Museum of Natural History, University of Kansas, Lawrence, Kan.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
PU	Princeton University Museum, Princeton University, Princeton, N. J.
UC	Museum of Paleontology, University of California, Berkeley, Calif.
USNM	United States National Museum, Washington, D. C.
YPM	Peabody Museum of Natural History, Yale University, New Haven, Conn.

REVIEW OF CLASSIFICATION

Families and Subfamilies

The family Anguidae was erected by Cope (1864, pp. 227–228) for lizards earlier grouped, on the basis of external characters, either with the Scincidae (*Diploglossus* and related genera) or with the Zonuridae (*Ophisaurus* and *Anguis*). In this first revision of the Diploglossa, Cope did not include the gerrhonotines in the family Anguidae, but granted them family rank as the Gerrhonotidae. The main criterion for Cope's action was the absence of a premaxillary foramen (located on the palatal junction of premaxilla and maxilla) in the gerrhonotines that was present in the other members of the Anguidae. He further subdivided his family Anguidae into four subfamilies on the basis of characters of the interclavicle (mesosternum of Cope) and the presence or absence of a lateral fold. The subfamilies were as follows:

(1) Diploglossinae, with no lateral fold and with elongated limbs of the interclavicle; including the South American *Diploglossus* and related forms. (2) Anguinae, with no lateral fold and with shortened interclavicle; only *Anguis fragilis* is included here. (3) Ophisaurinae, with a lateral fold and with interclavicle reduced or missing. Cope included here, along with the ophisaurs, the South American *Ophiodes* (=*Opheodes*), now included in the Diploglossinae. (4) Opheomorinae, without lateral fold (no character for the interclavicle given), contained only a single genus, *Opheomorus*, a name now applied to a group of African skinks.

Boulenger (1883, pp. 119–120) accepted Cope's conclusions in general, but listed no subfamilies and included the gerrhono-

tines in the family Anguidae. In 1885 he repeated the same classification, but described the anatomical characteristics of the family in more detail.

Cope (1900, pp. 488–492), influenced by Boulenger, included the gerrhonotines in the family Anguidae as one of the four subfamilies, and omitted the questionable Opheomorinae included among his earlier subfamilies. It is interesting to note that he here included *Ophiodes* in both Ophisaurinae and Anguinae (to neither of which this form belongs). Characters used for subdivision of the family were essentially the same as those utilized in the 1864 revision.

Camp (1923) did not go below the family level in his classification of lizards, but in considering a given family he referred to representative genera or species and to the relationship of these forms to one another within the family. His findings, especially with respect to the throat musculature, appear to support a close relationship between the ophisaurs and *Anguis*. "The Anniellidae are close to *Gerrhonotus* in structure of throat musculature and hemipenis. *Ophiodes* resembles *Celestus* in the former respect. *Gerrhonotus* and *Ophisaurus* are not as closely related as the latter is to *Anguis*" (Camp, 1923, p. 418; see also p. 373). Camp (1923, p. 340) also noted the resemblances between the hyoids of *Anguis* and *Ophisaurus*, in both of which (alone among anguids) all traces of the third arch are lost.

Camp (1923, pp. 327–329) also attempted to include fossil anguids in his classification and grouped them all, with the exception of the European fossil ophisaurs, in the extinct family Glyptosauridae of Marsh (1872). In this family he recognized four North American genera: *Xestops, Peltosaurus, Glyptosaurus, Helodermoides,* and questionably the European *Placosaurus.* Camp believed these fossils to represent an homogenous group, somewhat intermediate between the families Anguidae and Helodermatidae. He listed twelve characters in which the glyptosaurids differ from the former family, and twelve more characters in which they differ from the latter.

His characters separating the Glyptosauridae from the Helodermatidae are reprinted here (Camp, 1923, p. 328):

1. Presence of a supratemporal arch and fenestra
2. Separation of prefrontal and postfrontal above orbit
3. Postfrontal and postorbital entirely distinct
4. Pediculate caudal chevrons on the centra
5. A pineal foramen (very small in *Xestops*, absent in *Peltosaurus*)
6. Imbricated osteoderms on the body
7. Teeth on the pterygoid, palatine and prevomerine bones
8. Parietal united by suture (fused in *Peltosaurus*)
9. Transverse process of first caudal vertebra arising from the entire length of the centrum as in *Gerrhonotus*
10. Jugal with angular process
11. Frontals fused (separate in *Helodermoides*)
12. Teeth highly pleurodont with cylindrical, solid shafts and blunt, highly wrinkled crowns, as in some Anguidae.

Camp remarked that with the exception of unfused parietals, the above characters would allow the fossil forms to be included in the family Anguidae (in which he grouped the recent forms). Neither Gilmore (1928, p. 93) nor I found any trace of parietal suture in any Recent or fossil anguid (including Camp's Glyptosauridae). In addition, a parietal foramen is present in all fossil forms in which this region is preserved.

Camp's characters separating the Glyptosauridae and Anguidae are given as follows (Camp, 1923, p. 328):

1. The great extent of the patches of teeth on the pterygoid and palatines
2. The massive rectangular jugal, somewhat as in *Heloderma*
3. The extremely large tabulare, exposed dorsally as in *Heloderma*
4. The great length of the slender squamosal which extends forward nearly to the jugal
5. The corresponding reduction of the postorbital
6. The embossed tuberculate osteoderms slightly suggesting *Heloderma* in ornamentation
7. Quadrate peculiar in having a broad, thin, semicircular internal wing
8. Lower jaw massive; curved posteriorly as in *Heloderma*
9. Meckelian sulcus completely covered
10. Splenial extensive posteriorly
11. Angular with extensive external surface covering the surangular as a thin plate, somewhat as in *Gerrhonotus*
12. Paroccipital a separate element

Gilmore (1928, p. 93) dismissed Camp's reasons for not including the fossils in the family Anguidae as characters correlated with the large size of the fossils (points 2, 8), as applicable to some fossils only (1, 3, 7), as also present in the Recent forms (9, 10, 11), and the remaining as not of family significance. I believe that a number of Camp's glyptosaurid characters (e. g., 1, 3, 7, 12) were based on specimen AMNH 5168, and are not necessarily present or determinable in other fossils. This specimen was restored by Camp as *Xestops* and later was referred to a new genus *Melanosaurus* by Gilmore (1928, p. 138).

Kuhn (1940) gave a classification that resulted from a study on Middle Eocene anguids from Geiseltal, Germany. Kuhn distributed these fossil forms into two families in which he believed that two different trends existed. In one line, the Anguidae, a tendency toward limb reduction and body elongation occurred, as well as a tendency toward thinner osteoscutes. He recognized the following fossil and Recent forms as Anguidae: *Propseudopus, Pseudopus* (= *Ophisaurus*), *Eurosaurus, Anguis, Diploglossus, Melanosauroides, Ophipseudopus, Parapseudopus,* and *Ophisauriscus.*

In the other line, the Placosauridae, Kuhn saw no tendency toward limb reduction; the body is relatively short and the osteoscutes have well-developed tubercular sculpture. Here he includes: *Placosaurus, Glyptosaurus, Peltosaurus, Melanosaurus, Xestops, Placosauriops, Placosauroides,* and *Placotherium.* All members of this family are fossil.

McDowell and Bogert (1954) divided Recent and fossil members of the family Anguidae into four subfamilies: (1) Glyptosaurinae, (2) Gerrhonotinae, (3) Diploglossinae, and (4) Anguinae. Their conclusions regarding major characteristics of subfamilies and forms comprising these subfamilies are recapitulated below.

(1) The fossil Glyptosaurinae are the only anguids in which the following characters are exhibited: irregularly arranged and polygonal head osteoscutes, extremely large body size, and frontals widened in the interorbital region. This subfamily includes the North American genus *Glyptosaurus,* and the European *Placosaurus* and *Placotherium.* The first two generic names are probably synonymous.

(2) The Gerrhonotinae include *Gerrhonotus, Abronia, Coloptychon, Ophisaurus,* the fossil *Peltosaurus,* and perhaps also Kuhn's (1940) *Placosauriops* and *Placosauroides.* Members of this subfamily have rectangular scutes overlapping anteroposteriorly but sutured laterally, and an unossified fold is present between ventral and dorsal armor.

(3) In the Diploglossinae, no lateral fold is present, and there is no suturing between osteoscutes. The latter overlap laterally as well as anteroposteriorly, and conse-

quently the lateral surfaces are also beveled. The subfamily includes the Central and South American Recent anguids and the fossil *Xestops.*

(4) In the Anguinae, the single genus *Anguis* resembles the Diploglossinae in the above respects, but is distinguished from them in having fanglike dentition and a palate in which the anterior border of the palatine is in front of both the posterior extremity of the vomer and the anterior end of the interpterygoid vacuity.

Hoffstetter (1962a) examined osteoscutes of fossil and Recent anguids and concluded that on the basis of similar scutes and absence of lateral fold, the Anguinae and the Diploglossinae possibly should be combined in a single subfamily. Hoffstetter recognized only one other subfamily in the Anguidae, the Gerrhonotinae, in which he grouped Recent limbed gerrhonotines and ophisaurs and all extinct anguid genera. Hoffstetter listed the following fossil forms under the subfamily Gerrhonotinae: *Peltosaurus, Placosauriops, Placosauroides, Melanosaurus, Placosaurus, Glyptosaurus, Propseudopus, Parapseudopus, Ophipseudopus, Ophisauriscus,* and *Xestops.* He argued that all these forms exhibit the same type of robust, well-ossified, rectangular osteoscutes with well-developed gliding surfaces, and that these scutes may be sutured, beveled, or a combination of both along their lateral border.

The preceding historical treatment of anguid classification may be summarized as follows:

1. Since Cope's second classification (1900) there has been no disagreement as to what Recent forms belong in the family Anguidae.
2. In the three major attempts to divide the family into subfamilies (Cope, 1900; McDowell and Bogert, 1954; and Hoffstetter, 1962a), body scutellation and the presence or absence of a lateral fold have been heavily relied upon, especially by the latter two authors.
3. On two occasions (Camp, 1923; Kuhn, 1940) the large Eocene and Oligocene forms were considered an homogenous group and transferred from the Anguidae into a separate family (Camp's Glyptosauridae and Kuhn's Placosauridae).

Recent Genera and Subgenera

Tihen (1949) examined skull structure and scutellation in the limbed gerrhonotines, and on the basis of these characters recognized five genera within this group: *Coloptychon, Abronia, Gerrhonotus, Elgaria,* and *Barisia.* He also supported the inclusion of the fossil *Melanosaurus* and *Peltosaurus* in the subfamily Gerrhonotinae.

Stebbins (1958) described a new species of alligator lizard, *Gerrhonotus panamintinus.* In order to determine the taxonomic position of the new lizard, Stebbins re-examined Tihen's genera. He found that the *Elgaria-Gerrhonotus* group is generally oviparous and the *Barisia* group ovoviviparous. However, *Elgaria coerulea* is ovoviviparous, and this form exhibits a number of characters (scutellation, pigmentation, and number of pterygoid teeth) intermediate between the genera *Barisia* and *Elgaria.* In view of the intergradation among the above genera, Stebbins proposed to group three of Tihen's genera (*Elgaria, Gerrhonotus,* and *Barisia*) into a single genus *Gerrhonotus* with two subgenera, *Barisia* and *Gerrhonotus* (the latter including *G. liocephalus* and members of the genus *Elgaria*). Stebbins regarded the characters given by Tihen as insufficient for generic (or even subgeneric) separation of *Elgaria* and *Gerrhonotus* and referred them both to the subgenus *Gerrhonotus.* Bogert and Parker (1967) considered *Barisia* a genus for purposes of their discussion. Criley (1968) examined osteological characters of gerrhonotiform lizards and concluded that it is impossible to support *Barisia* and *Elgaria* on an osteological basis, either as genera or as subgenera.

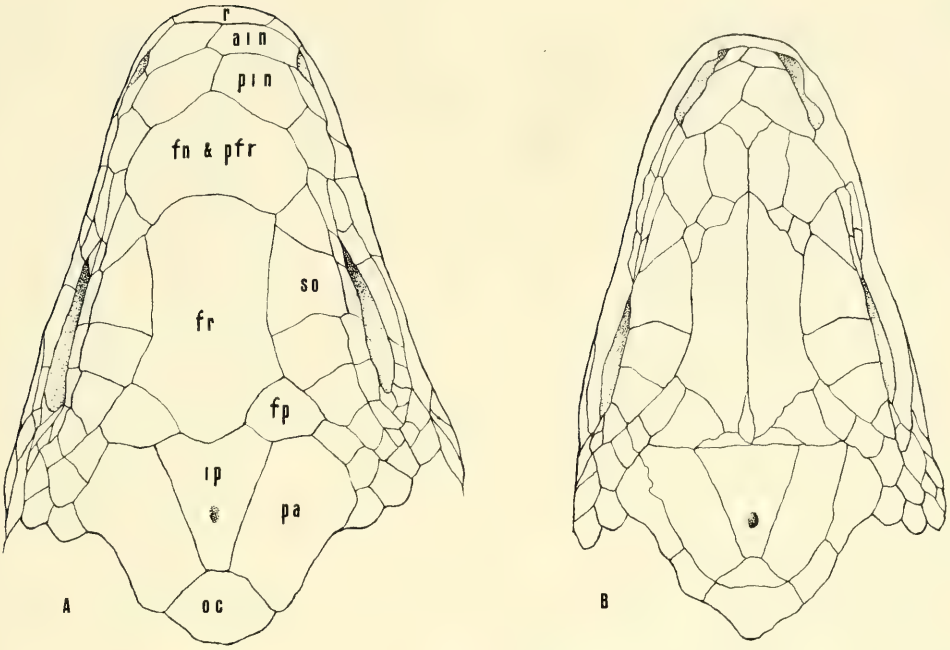

Figure 1. Lack of correspondence between cranial osteoscutes and epidermal scales: A, head of *Diploglossus hewardii*, MCZ 45170, Recent, with epidermal scales; B, the same with epidermal scales removed, exposing osteoscutes; both × 4. The skull in B is shrunken because of desiccation. For abbreviation see p. 147.

McConkey (1954) examined North American members of the genus *Ophisaurus* and recognized three distinct species on the basis of scutellation and ratio of body to tail length: *O. ventralis*, *O. compressus*, and *O. attenuatus*. In the last he distinguished two subspecies, *attenuatus* and *longicaudus*. McConkey later (1955) described a new species, *O. incomptus*, from Mexico. Holman (1965) added another new species, *O. ceroni*, also from Mexico. Five other species of *Ophisaurus* are known from Eurasia and Africa: *O. apodus*, *O. buttikoferi*, *O. gracilis*, *O. harti*, and *O. koellikeri*.

Underwood (1959) revised the subfamily Diploglossinae, members of which occur in South America and the West Indian Islands. In the past, South American forms had been placed in the genus *Diploglossus*, whereas island forms were referred to the genus *Celestus*. The criterion of distinction used by Burt and Burt (1931) was the presence of claw sheaths and three prefrontal epidermal scales (1 frontonasal and 2 prefrontals of this paper, Fig. 1) in the former; no claw sheaths and a single prefrontal in the latter. Underwood found overlap in both these characters; three island forms have a claw sheath (*D. delasagra*, *D. pleei*, and *D. microblepharis*), and *D.* (=*Sauresia*) *sepsoides* and *D. darlingtoni* occasionally have 3 prefrontals. Therefore he regarded both *Celestus* and *Sauresia* as members of the genus *Diploglossus*. Underwood (1964) described a new species, *Diploglossus montiserrati*, from the Leeward Islands. This lizard resembles the "typical" mainland forms (especially *D. monotropis*), thus further tending to de-emphasize the distinctions between island and mainland forms.

In this paper, I shall use the generic classification of Stebbins (1958), McConkey (1954), and Underwood (1959) for the Recent anguids.

DESCRIPTION OF RECENT ANGUID GENERA

Anguids do not contribute extensively to the present-day herpetological fauna either in number of individuals or in number of species. There are approximately 62 species of Recent anguids recognized currently, distributed among seven genera. The family contains arboreal forms (members of the genus *Abronia*) and limbless semiburrowers (*Ophisaurus*, *Anguis*, and *Ophiodes*); the rest of the genera are terrestrial. Anguids at present occur in Palearctic, Nearctic, Neotropical, and Oriental geographical realms, with only limbless forms in the Old World continents, and only one genus, *Ophisaurus*, occurring both in the Old and the New World.

Living anguid genera fall into four general groupings: (1) the North and Central American *Gerrhonotus* and *Abronia*, (2) the North American and Eurasian ophisaurs, (3) the European monotypic *Anguis*, and (4) the South and Central American *Diploglossus*, *Wetmorena*, and *Ophiodes*. These four groups correspond essentially to Cope's (1900) subfamilies, with *Ophiodes* is placed in the diploglossines. Consideration of each of these groups as a unit facilitates discussion of the distribution of osteological and scutellation character-states among Recent anguids; a subfamilial classification will follow the discussion of fossil genera.

Anguis fragilis

Osteological material. (3) *Anguis fragilis*, MCZ 1032, 3958, 37174.

Skull: Teeth with unstriated crowns, recurved, fanglike, and widely spaced; five to seven teeth in each maxilla and dentary; palatal bones edentulous pterygoids; slender, widely separated from one another at the midline, and with elongated palatine processes (measuring one-third of the total length of the pterygoid); premaxillary foramina present at union of premaxilla and maxilla (Fig. 2c). Frontals not fused, orbital borders almost straight and not in contact with maxilla; olfactory process of frontal not in contact with dorsal process of palatine; body of parietal and frontal of approximately equal length; parietal foramen present; postfrontal and postorbital distinct, with postorbital excluded from the orbit; jugal with only a suggestion of a posterior process. Surangular and articular unfused, with surangular extending well beyond well-developed anterior process of coronoid on the labial surface of the dentary (Fig. 3a); dentary not in contact with anterior supra-angular foramen; both dentary and splenial participate in formation of anterior inferior alveolar foramen (Fig. 4a).

Vertebrae: 62 presacrals (not including atlas and axis), 61 with ribs and first four with ventromedial hypapophysial processes; single sacral; first caudals with hemal arch bases indistinguishably fused to centra; ribs with tubera costarum.

Individual presacral vertebrae procoelous, elongate, flattened ventrally with prominent paired subcentral foramina; lateral margins slightly concave in ventral view (Fig. 5d). Condyles large, flattened ventrally, slightly exceeding breadth of centrum immediately before condyle; condylar head with little ventral exposure. Neural spines moderately low with weblike process on leading edge of spine. Single sacral with forked, lobsterclaw-shaped transverse process slightly curved posteriad; anterior prong of fork distally much larger than posterior.

Caudals less concave than presacrals, with relatively narrower centra and chevrons indistinguishably fused to centra. Bases of transverse processes often bifurcate and the autotomy plane well marked, extending across vertebra in an arch between the bases of transverse processes.

Epidermal scalation: Frontonasal and frontal in narrow contact; frontal and interparietal in very broad contact, widely separating the small frontoparietals; interparietal large and in narrow contact with small occipital.

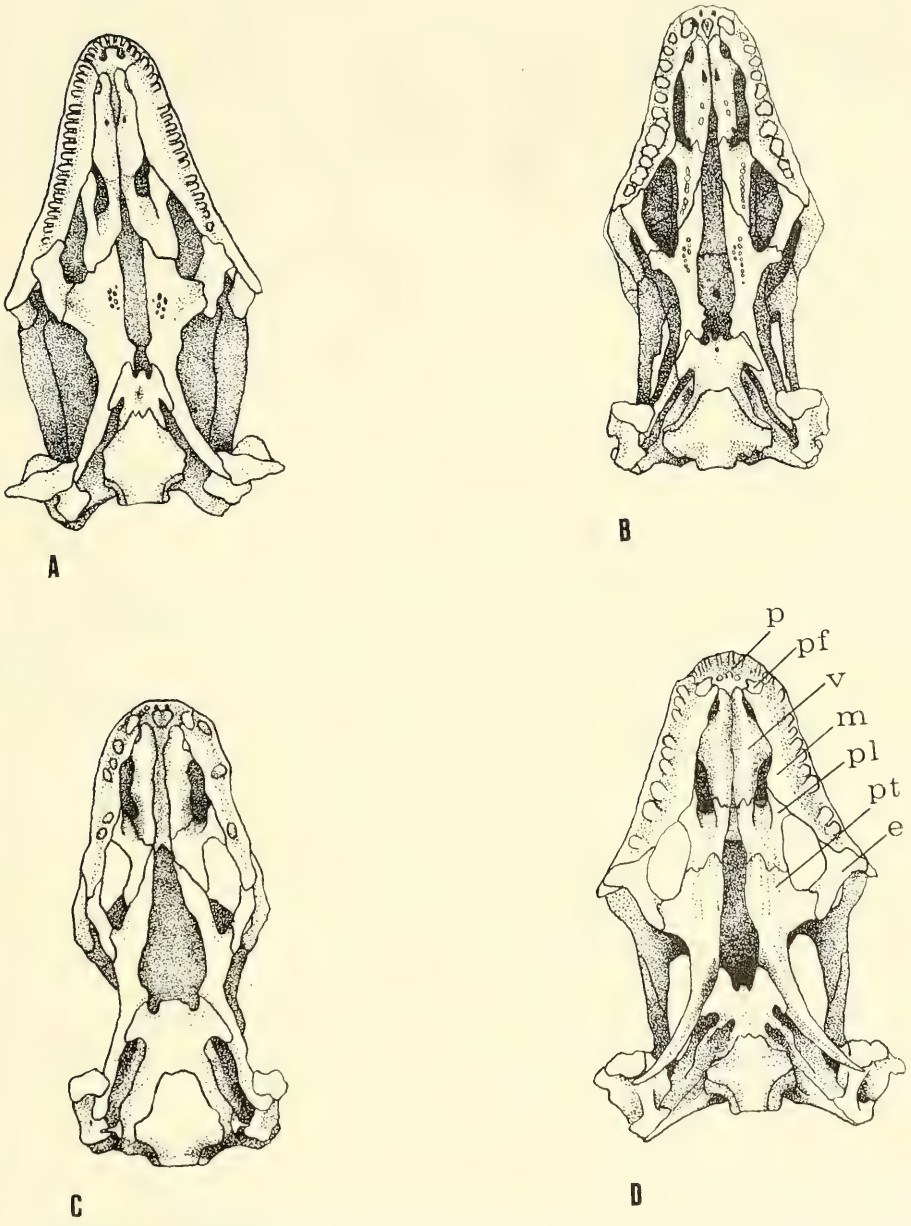

Figure 2. Skulls of recent anguids in ventral view: A, *Gerrhonotus liocephalus*, MCZ 19062; B, *Ophisaurus apodus*, MCZ 2094a; C, *Anguis fragilis*, MCZ 37174; D, *Diploglossus occiduus*, BM(NH) 63.2.21.17. Note presence of large premaxillary foramen in all except *Gerrhonotus*, at junction of premaxilla with maxilla. A × 2, B × 1.5, C × 4 and D × 1.25. For abbreviations see p. 147.

Body scales unkeeled, smooth; *in situ* wider than long; no lateral fold.

Body osteoscutes: Thin with rounded outlines; middorsals almost round with halfmoon-shaped, lateroposteriorly-recurved gliding surfaces (Fig. 6c). Laterals elliptical with gliding surface extending along almost entire left or right edge of osteo-

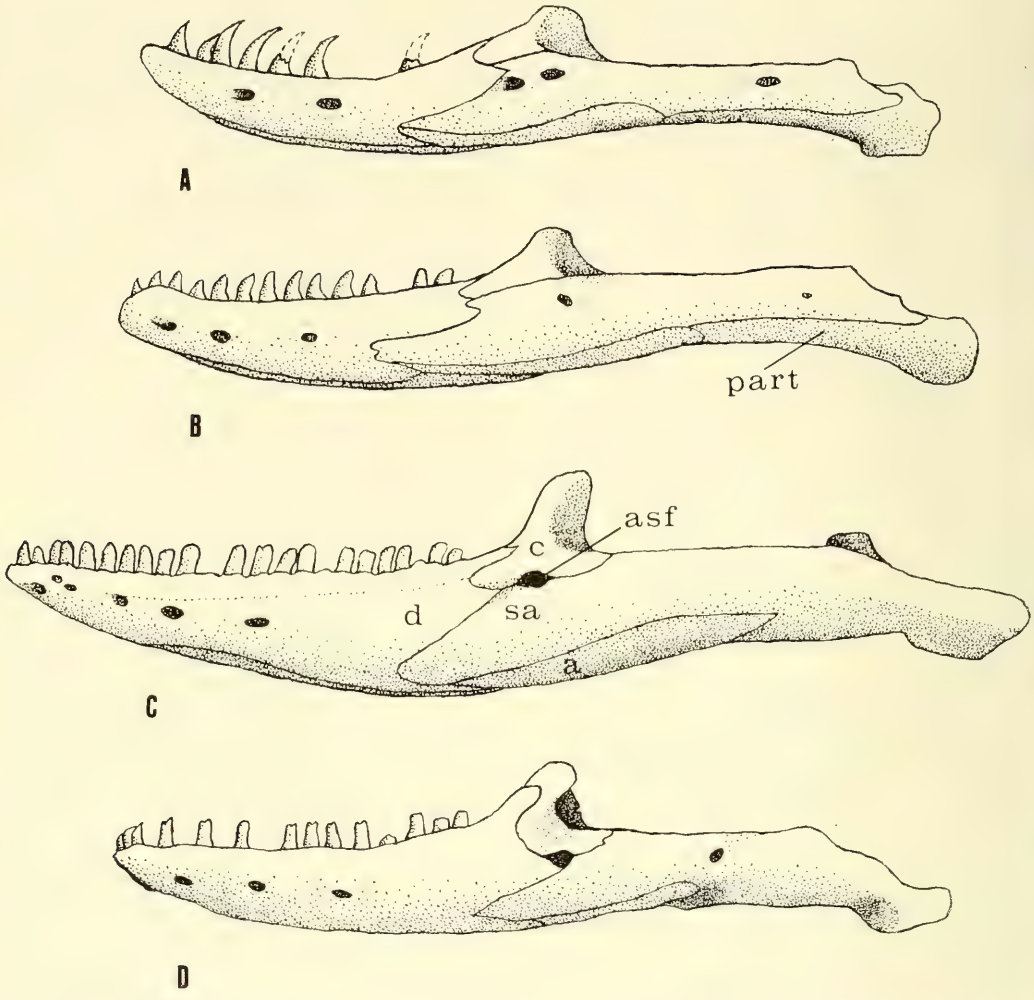

Figure 3. Mandibles of recent anguids in labial view: A, *Anguis fragilis*, MCZ 37174; B, *Ophisaurus gracilis*, MCZ 15836; C, *Gerrhonotus (Barisia) imbricatus imbricatus*, MCZ 97400; D, *Diploglossus barbouri*, MCZ 7367a. Note resemblance between A and B and also note that in all forms surangular exceeds coronoid anteriorly. All × 6. For abbreviations see p. 147.

scute (depending on side of origin) and becoming confluent with lateral bevel. Midventrals with greatest width along the gliding surface, becoming narrower posteriorly.

Ophisaurus

Osteological material. (4) *Ophisaurus apodus*, MCZ 32249, 2094, AMNH 75481, 73228; (2) *O. attenuatus*, MCZ 5548a-b; (1) *O. compressus*, MCZ 12825; (1) *O. gracilis*, MCZ 15836; (1) *O. harti*, MCZ 46916; (1) *O. koellikeri*, MCZ 61138; (4) *O. ventralis*, MCZ 620, 32258, 55509, 1949.

Skull: Teeth ranging from blunt-crowned, robust crushing teeth in *Ophisaurus apodus* to recurved, widely-spaced, fanglike types with pointed apices and unstriated crowns in *O. harti*. Teeth in general more pointed and less chisel-shaped (especially in the Old World forms) than in *Gerrhonotus* or *Diploglossus* and allies; palatal teeth pres-

ent on pterygoid and palatine on all examined species. Auffenberg (1955, p. 133) indicates that teeth are absent from the palatine bone in *O. attenuatus;* in both MCZ specimens of *O. attenuatus attenuatus* available to me, however, teeth were present on the palatine bone (Fig. 2b). In *Ophisaurus apodus* teeth also present on vomers; palatine teeth arranged either in rows or patches; pterygoids slender, widely separated, with elongated palatine processes (measuring at least one-third of total length of pterygoid). Premaxillary foramina present; frontals unfused, with almost straight orbital borders, not in contact with maxilla; olfactory process of frontal not in contact with dorsal process of palatine except in *O. gracilis;* parietal foramen present; postorbitals and postfrontals distinct, with postorbital excluded from orbit; surangular and articular distinct in *Ophisaurus apodus* and *O. harti;* surangular well in advance of the anterior coronoid process; anterior labial process of coronoid well developed (except in *Ophisaurus apodus,* in which backward extension of dentary prevents development of this process, paralleling the situation noted for *Diploglossus* and related forms). Both dentary and splenial involved in formation of anterior inferior alveolar foramen (Fig. 4d). Anterior supra-angular foramen labially placed, not in contact with dentary (Fig. 3b).

Vertebrae: Presacrals (not including atlas and axis) in the mid-fifties, excepting *Ophisaurus compressus* with 44; only available counts, *O. apodus* (52–53), *O. attenuatus attenuatus* (56–57), *O. a. longicaudus* (54), *O. harti* (55), *O. ventralis* (57). Single sacral; first caudal with hemal arch bases indistinguishably fused to centra. Ribs with tubera costarum.

Individual presacral vertebrae ventrally flattened with paired subcentral foramina (Fig. 5c); neural spine angles made with centrum more acute than in *Anguis fragilis;* anterior weblike extension on leading edge of spine little developed. Condyle large with little ventral exposure. Single sacral with bifurcated, posteriad-directed, lobsterclaw-like transverse process as in *Anguis.* Caudal chevrons indistinguishably fused to centra.

Epidermal scalation: Frontonasal and frontal contact variable in the genus; the above scales in narrow contact in *Ophisaurus apodus, O. gracilis,* and *O. ventralis* (variation probably occurs in all forms, as noted by McConkey, 1954, pp. 142, 147, 150; tables 1a, 2a, 3a); no frontal contact in *O. attenuatus, O. ceroni* (from Holman, 1965) or *O. buttikoferi;* contact highly variable in *O. harti;* in two small *O. koellikeri* frontonasal fused with the two lateral prefrontals, in a single large specimen frontonasal distinct and in contact with frontal. In all, contact is wide between frontal and interparietal, and consequently the small interparietals are widely separated. Interparietal large and in narrow contact with small occipital.

Body scales wider than long, keeled in *Ophisaurus apodus, O. attenuatus, O. ceroni* (from Holman, 1965), *O. harti, O. koellikeri, O. ventralis;* lateral fold present in all.

Body osteoscutes: Much thicker than in *Anguis* and more angular (Fig. 6b). Lateral osteoscutes with bevel along their lateral edges; gliding surface occupying less than one-half total length of scute and with appearance of a transverse band; middorsals fanned out posteriad, with bevels along both lateral surfaces; midventrals wedge-shaped, with less prominent bevels along ventrolateral edges.

Gerrhonotus and Abronia

Osteological material. (1) *Abronia deppii,* MCZ unnumbered specimen. (1) *Gerrhonotus coeruleus,* MCZ 999; (2) *G. kingi,* MCZ 14834, 1452; (3) *G. liocephalus,* MCZ 24514a-c; (4) *G. multicarinatus,* MCZ 32250, 63657, and two unnumbered; (1) *G. imbricatus,* MCZ 97400; (1) *G. monticolus,* MCZ 15467; (1) *G. moreleti,* MCZ 49958.

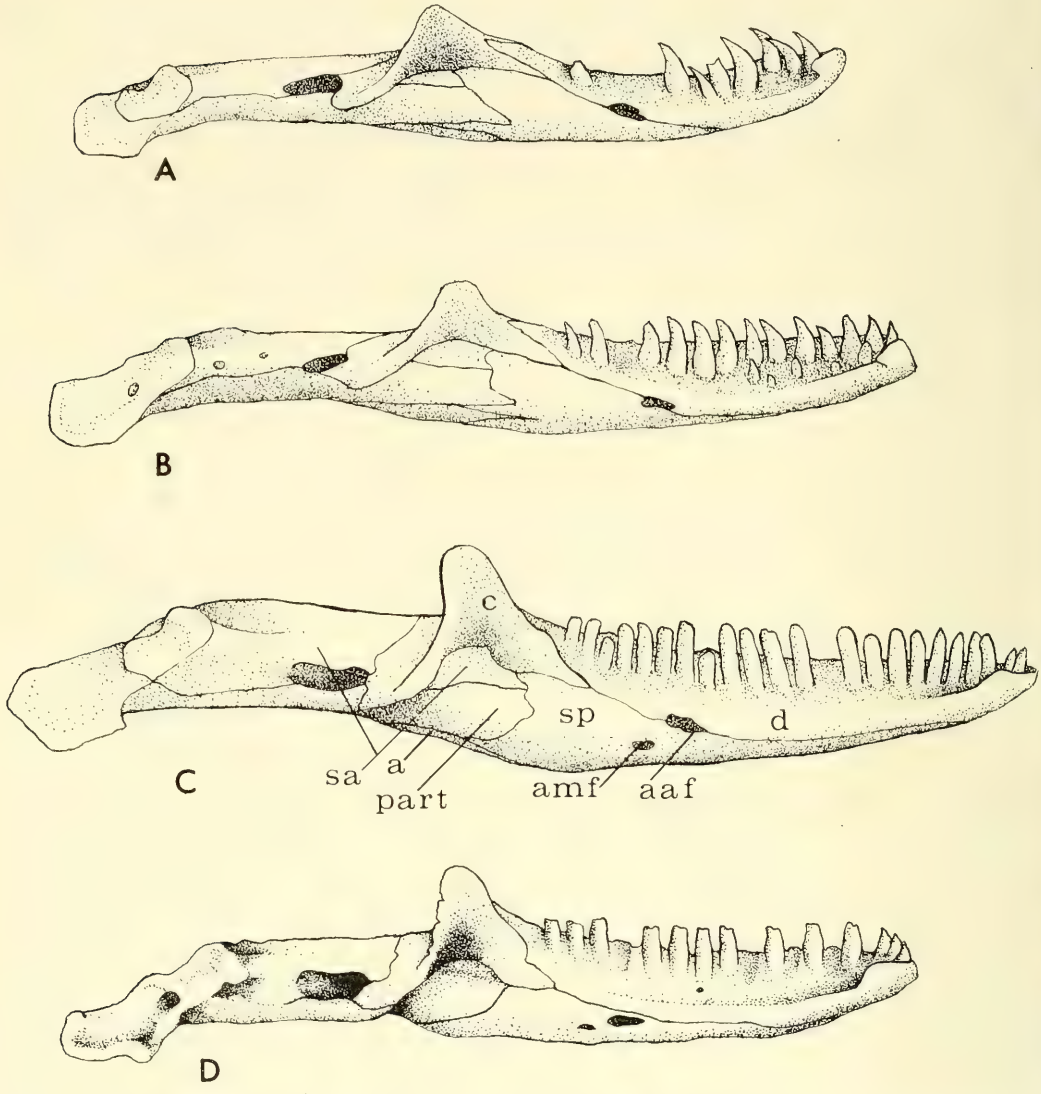

Figure 4. Mandibles of recent anguids in lingual view: A, *Anguis fragilis*, MCZ 37174; B, *Ophisaurus gracilis*, MCZ 15836; C, *Gerrhonotus (Barisia) imbricatus imbricatus*, MCZ 97400; D, *Diploglossus barbouri*, MCZ 7367a. Note that in formation of the anterior inferior alveolar mental foramen the dentary takes part in all except *Diploglossus*. All × 6. For abbreviations see p. 147.

Skull: Teeth in most species of *Gerrhonotus* recurved and somewhat pointed in anterior part of jaws, but becoming erect with chisel-shaped, laterally compressed crowns posteriad. *Abronia* has pointed, widely spaced teeth (but not to the extent observed in *Anguis* or in *Ophisaurus harti*). Pterygoids toothed in *G.* (*Gerrhonotus*) and rarely in *G.* (*Barisia*); pterygoids robust with short palatine processes, closely approaching each other in *G. liocephalus* (Fig. 2a), widely separated in *Abronia*, and intermediate in *G.* (*Barisia*) and other *G.* (*Gerrhonotus*). No premaxillary foramina;

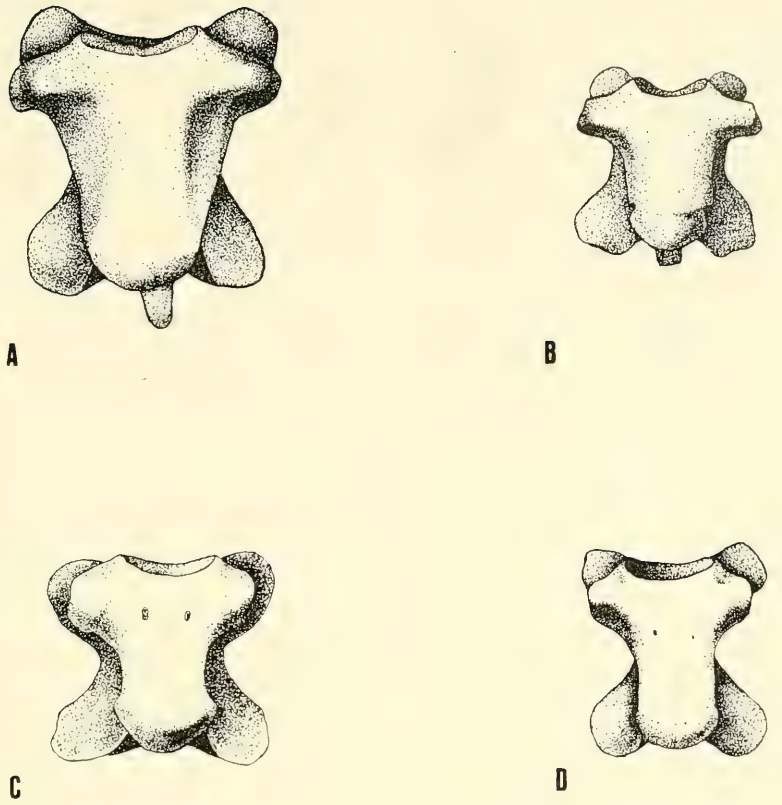

Figure 5. Trunk vertebrae of some anguids in ventral view: A, *Diploglossus monotropis*, MCZ 22912; B, *Gerrhonotus multicarinatus*, MCZ, unnumbered; C, *Ophisaurus ventralis*, MCZ 55509; D, *Anguis fragilis*, MCZ 37174. Note ventrally flattened centra in C and D, small exposure of condylar ball in A; not to scale.

frontals fused with concave orbital borders; olfactory process of frontal in contact with dorsal process of palatine bone. Maxilla and frontal in contact in *G. liocephalus* and also in the single specimen of *Abronia deppii* (Tihen, 1949, states that frontals are narrowly separated from maxilla in *Abronia*); parietal foramen present; postfrontal and postorbital separate, with postorbital gaining narrow exit into the orbit; jugal with well-developed posterior process. Surangular and articular usually fused, but the two bones may be separate or fused intraspecifically in *G. kingi;* surangular well or moderately in advance of labial dentary process of coronoid; labial dentary process of coronoid well developed in all members of *Gerrhonotus* (Fig. 3c) and *Abronia;* anterior inferior alveolar foramen bordered above by dentary, below by splenial; anterior supra-angular foramen on labial surface not in contact with dentary (Fig. 4c).

Vertebrae: About 30 presacral vertebrae (Fig. 5b). Counts were possible on only the following species: *Abronia deppii* (27), *Gerrhonotus coeruleus* (26), *G. kingi* (30), *G. monticolus* (27), *G. moreleti* (26). Two sacrals with distal ends of transverse processes in contact; first caudals with chevrons located on pedicels; pedicels located on centrum right next to or confluent with condyle. Ribs without tubera costarum.

Epidermal scalation: No frontonasal and

frontal contact in most; in some species of subgenus *G.* (*Barisia*) no azygous frontonasal present at all. Frontonasal and frontal contact observed in: *Gerrhonotus liocephalus infernalis, G. monticolus, G. moreleti temporalis,* and *G. m. salvadorensis.* Left and right frontoparietals closely approaching each other or in narrow contact, as in *G. liocephalus loweryi, G. liocephalus infernalis, G. coeruleus,* and *Abronia deppii;* interparietal and occipital contact in all.

Body scales arranged in transverse bands, dorsals often with keels; lateral fold present in *Gerrhonotus,* but weakly developed or absent in *Abronia.*

Osteoscutes: Rectangular with gliding surface well developed in *Gerrhonotus,* but degenerate in *Abronia.* Gliding surface in shape of anterior transverse band. Lateral bevels prominent and indicative of overlap between adjacent osteoscutes. No lateral suturing present between osteoscutes.

Diploglossus, Wetmorena, and *Ophiodes*

Osteological material. (2) *Diploglossus monotropis,* MCZ 29682, 22912; (1) *D. badius,* MCZ 55722; (2) *D. barbouri,* MCZ 3767-a, 3767-c; (3) *D. costatus,* MCZ 63562, 65069, 65006; (3) *D. crusculus,* MCZ 7355, 45208, and one with no number; (1) *D. darlingtoni,* MCZ 57750; (1) *D. d. delasagra,* MCZ 38597; (3) *D. hewardi,* MCZ 7356, 7366, and one with no number; (7) *D. pleeii,* MCZ 36233, 36253 and five with no numbers; (1) *D. sepsoides,* MCZ 57056. (1) *Wetmorena haetiana,* MCZ 38270. (2) *Ophiodes striatus,* MCZ 20669, 7271.

Skull: Teeth ranging in these forms from robust crushing type with blunt crowns, as in *Diploglossus montiserrati* and *D. crusculus maculatus,* to teeth with pointed apices in *Ophiodes striatus;* in majority of forms teeth moderately robust with laterally compressed, chisel-shaped cutting edges; in all examined forms crowns with striations; no teeth on palate (Fig. 2d); pterygoids robust, closely approaching one another on midline; premaxillary foramina present; frontals separate; dorsal process of palatine in contact with olfactory process of frontal; parietal foramen present; postorbitals and postfrontals in most forms distinct, but fused in *Ophiodes* and *Diploglossus pleeii,* with postfrontal entering into the orbit; jugal with well-developed posterior process, except in *Ophiodes* where it is ill-defined; surangular, prearticular, and articular usually fused (Fig. 3d), with unfused condition occurring sporadically; surangular in advance of anterior coronoid process; anterior labial process of coronoid not well developed and dorsal process well forward on this bone because of backward extension of the dentary; anterior inferior alveolar foramen of mandible bounded above and below by splenial (Fig. 4b). Anterior supra-angular foramen on the labial surface in contact with the dentary.

Vertebrae: Presacrals in thirties and forties in *Diploglossus,* but 72–74 in *Ophiodes striatus.* The following individual counts have been made: *Diploglossus barbouri* (34), *D. badius* (33), *D. costatus* (31), *D. crusculus* (33), *D. monotropis* (32), *D. d. delasagra* (43), *D. pleeii* (40), *D. sepsoides* (38). Two sacrals with distal end of transverse processes in close contact, even in the limbless *Ophiodes striatus.* Chevrons not fused to sacral vertebrae but joined to short, stubby pedicels. Ribs lacking tubera costarum in all species including *O. striatus.*

Centra of individual presacrals triangular in ventral view, not flattened but central portion slightly raised, slight constriction present between centrum and condyle (Fig. 5a). Caudals with unfused chevrons attached to pedicels, the latter somewhat removed from the condyle but closer to it than in *Ophisaurus* or *Anguis.*

Head scalation (Fig. 1): Frontonasal when present in contact with frontal; in *Ophiodes* as well as in all island forms frontonasal and two prefrontals fused (with a single exception noted by Underwood, 1959, p. 7). In holotype of *Diploglossus darlingtoni* these three scales

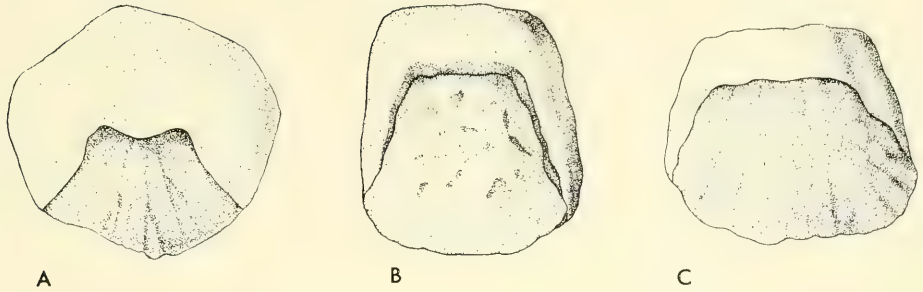

Figure 6. Middorsal body osteoscutes of recent anguids: A, *Diploglossus monotropis*, MCZ 29682, × 8; B, *Ophisaurus attenuatus attenuatus*, MCZ 5548b, × 17; C, *Anguis fragilis*, MCZ 3958, × 17. Note close resemblance between B and C, and unique medial convexity of gliding surface of A, occurring only in Diploglossinae.

separate, but fused in other specimens; frontoparietals widely separated, but not to the extent noted for *Ophisaurus* or *Anguis;* scales relatively much larger than in latter two genera; interparietal large, in contact with small occipital.

Body scales: *In situ* cycloid, skink-like in general appearance; lateral fold absent; keels present in a number of species, e.g., *D. monotropis, D. hewardi;* keels absent in *O. striatus.*

Body osteoscutes: With rounded outlines; anterior smooth gliding surface semicircular with posteromedial peak directed into sculptured surface that is especially prominent in dorsomedial scutes (Fig. 6a).

Discussion. Gerrhonotus and *Abronia* exhibit a number of cranial characters that are in strong contrast to conditions found in other Recent anguids. The unique premaxillary foramen of other Recent anguids is absent in these two genera (Fig. 2). In addition, fused frontals with prominent concave borders are found only in *Gerrhonotus* and *Abronia*, and here alone do the frontoparietal scales make a narrow contact (Fig. 12b). These two genera (especially *Gerrhonotus*) do, however, have body osteoscutes essentially the same as those in *Ophisaurus.* In both of these groups the osteoscutes are thick, bony, and rectangular, with a well-defined gliding surface in the shape of an anterior transverse band. These osteoscutes are beveled laterally where adjacent scutes overlapped, and no visible evidence of suturing between osteoscutes occurs. Both ophisaurs and *Gerrhonotus* have a lateral fold that connects the dorsal and ventral armor and apparently allows for greater mobility in these heavily armored forms. Where osteoscutes are not well developed, as in *Abronia*, the lateral fold is weak or absent.

Aside from body scutellation and the presence of teeth on the pterygoids, *Ophisaurus* shows no special resemblance to *Gerrhonotus.* However, the ophisaurs do have a great number of characters in common with *Anguis fragilis* that sets them apart from other anguids: (1) the postorbital is excluded from the orbit; (2) the olfactory process of the frontals fails to meet the dorsal process of the palatine; (3) the palatine process of the pterygoid is placed well anteriad of the maxillary process of the same bone, and the former process exceeds one-third the total length of the pterygoid; (4) the ribs have proximal posterior processes (tubera costarum) for muscle attachment; (5) only a single functional sacral vertebra, of similar shape, is present in both *Anguis* and *Ophisaurus;* (6) the caudal vertebrae have hemal arches fused to centra; (7) the frontoparietal scales are small and placed well laterad; (8) there is a close resemblance between the mandibles of the two genera in regard to proportion of dentary to post-dentary

portion and in regard to sutural contact between the above parts (Fig. 3a-b). Other characters not unique to the above forms, but shared with *Diploglossus* are: (1) paired frontals; (2) premaxillary foramen present. Also in *Anguis* as well as in *Ophisaurus*, but not in *Diploglossus*, and shared with some species of *Gerrhonotus*, the maxilla is not in contact with the frontal.

The main reason given by McDowell and Bogert (1954, p. 130, fig. 43) for placing *Anguis* in a subfamily of its own, the Anguinae, was the absence of a lateral fold and the superficially *Diploglossus*-like body scalation. However, this condition was regarded as degenerate by these authors, and they regarded the slow-worm as a specialized derivative of the ophisaurs. It is true that neither *Diploglossus* nor *Anguis* has a lateral fold, but the resemblance in osteoscutes is superficial. The isolated osteoscutes of *Diploglossus* are in strong contrast to those of *Anguis* and all other Recent anguids. Only in the diploglossines does the posterior margin of the much enlarged gliding surface have a posteriorly-directed peak (Fig. 6) where it meets the sculptured area of the osteoscutes. The osteoscutes of *Anguis* may be regarded as degenerate ophisaurine scutes in which the scutes are less rectangular, thinner, and have less prominent gliding surfaces. *Anguis* also exhibits a number of other degenerate features: lack of teeth on the palate, further reduced limb girdles, and absence of an external ear opening (also lacking in *O. koellikeri*). Further support of a close relationship between the ophisaurs and *Anguis* comes from Camp's studies on throat musculature (1923, p. 373), in which he states: "*Ophisaurus anguis* and *Anguis fragilis* are similar to each other and somewhat different from both *Ophiodes* and *Gerrhonotus*." He also notes (p. 340) that only in *Anguis* and *Ophisaurus* are all traces of the third branchial arches of the visceral skeleton lost. That the great number of characters common for both *Ophisaurus* and *Anguis* is not the result of convergence due to limblessness is supported by the fact that the limbless diploglossine *Ophiodes* displays none of them. However, ventrally flattened vertebral centra and pointed recurved teeth appear to be specializations associated with limbless existence. Aside from *Abronia*, pointed teeth occur only in the limbless anguids, and all these forms have ventrally-flattened vertebral centra. The ophisaurs exhibit the greatest number of characters that may be regarded with some certainty as primitive for anguids as well as for all lizards, including paired frontals, teeth on palatines, pterygoids, and vomers. Vomerine teeth occur only in *Ophisaurus apodus*. Also, the ophisaurs appear to be somewhat intermediate between *Gerrhonotus* and the diploglossines. The ophisaurs share a similar body scutellation, the presence of a lateral fold, and a toothed pterygoid with the former group, and the presence of a premaxillary foramen and paired frontals with straight orbital borders with the latter.

The diploglossines differ from the ophisaurs and *Anguis* in the eight points in common listed above, and from *Abronia* and *Gerrhonotus* in having a premaxilliary foramen, paired frontals, and no lateral fold. They differ from all other anguids in having unique osteoscutes, with the posterior margin of the gliding surface having a posteriorly-directed peak, in having the anterior inferior alveolar foramen wholly on the splenial, and a tendency toward postorbital and postfrontal fusion. The diploglossines appear to be degenerate in the complete loss of palatal teeth in all members.

From this survey of Recent anguids, it appears that body scutellation is similar in the different groups of Recent anguids, and is evidence not always in accord with that from cranial and postcranial osteology. Scutellation in anguid classification should be utilized only in conjunction with evidence from osteology and soft anatomy.

Summary. (1) *Anguis* and *Ophisaurus*

are very closely related, in spite of different body scutellation in the two forms and the absence of a lateral fold in *Anguis*.

(2) *Ophisaurus* exhibits characters intermediate between the diploglossines and the Recent limbed gerrhonotines, sharing the separate frontals and the presence of a premaxillary foramen with the former and a similar body scutellation, lateral fold, and toothed palatal elements with the latter.

(3) The osteoscutes of the diploglossines are unique among Recent anguids. The osteoscutes of *Ophisaurus* and *Gerrhonotus* are similar, and those of *Anguis* represent a highly degenerate version of this type. Osteoscutes of all fossil anguids resemble those of *Ophisaurus* and *Gerrhonotus*.

(4) There is no justification for regarding the ophisaurs as closer related either to the limbed gerrhonotines or to the diploglossines, or to group these forms in the same subfamily with either of the above.

(5) On the basis of data presented above, the Recent forms are best divided into three subfamilies:

a) The Gerrhonotinae (including the Recent limbed gerrhonotines of this paper, *Gerrhonotus, Abronia,* and tentatively *Coloptychon;* the type and only specimen of the latter, in the Humboldt Museum, Berlin, is lost).

b) The Diploglossinae (including *Diploglossus, Ophiodes,* and *Wetmorena*).

c) The Anguinae (including the genera *Ophisaurus and Anguis*).

It is now of interest to see whether or not the fossil forms can be placed in this classification, and what modifications they may suggest.

DESCRIBED NORTH AMERICAN FOSSIL GENERA AND SPECIES

Gervais (1859) was the first to describe a fossil referable to the Anguidae. He gave the name *Placosaurus rugosus* to a specimen (from the Upper Eocene of Sainte Aldegarde, France) consisting of skull fragments and osteoscutes. Similar fossils from Europe were described under the names of *Diploglossus cadurcensis* de Stefano (1904), *Plestiodon cadurcensis, Necrodasypus galliae* Filhol (1877, 1894), and *Varanus margariticeps* Gervais (1876). Boulenger (1918) regarded all of these fossils as placosaurs.

The first to describe fossil anguids from North America was Marsh (1871). He referred Middle Eocene fossil remains from the Bridger Formation of Wyoming to a new genus with four species: *Glyptosaurus sylvestris, G. ocellatus, G. nodosus,* and *G. anceps.* Marsh (1872, p. 6) added a further new species, *G. princeps,* and in the same paper described *Oreosaurus vagans* (the preoccupied generic name *Oreosaurus* was later changed to *Xestops* by Cope, 1873). In Part II of the same paper Marsh added three more species to *Glyptosaurus* and four more to *Xestops* (=*Oreosaurus*). Gilmore (1928, p. 94) synonymized *G. ocellatus* with *G. sylvestris* and referred *G. anceps* to the Amphisbaenidae. With the exception of *X. vagans,* the specimens referred to *Xestops* by Marsh consist of very fragmentary lower jaws, vertebrae, and osteoscutes. Marsh made no reference as to where among the Recent families the affinity of the fossils lay, but considered *Glyptosaurus* and *Xestops* as related forms.

Cope (1873, p. 5) described a new genus and species, *Peltosaurus granulosus,* from the Oligocene Cedar Creek beds of Colorado, and later (1884, p. 772) referred the fossils to his family Gerrhonotidae (see above).

Gilmore (1928) was the first to study all available North American fossil lizard material and to examine the interrelationships among the fossil forms and their affinities to Recent groups. Gilmore recognized four fossil genera in the family Anguidae and the following species under these genera:

Glyptosaurus sylvestris Marsh 1871

G. nodosus Marsh 1871
G. princeps Marsh 1872
G. rugosus Marsh 1872
G. sphenodon Marsh 1872
G. tuberculatus Douglass 1903
G. obtusidens Loomis 1907
G. montanus Douglass 1908
G. hillsi Gilmore 1928
G. giganteus Gilmore 1928
Peltosaurus granulosus Cope 1873
P. abbottii Gilmore 1928
P. (?) *piger* Gilmore 1928
Xestops vagans Marsh 1872
X. (?) *gracilis* Marsh 1872
X. (?) *lentus* Marsh 1872
X. (?) *microdus* Marsh 1872
X. (?) *minutus* Marsh 1872
X. (?) *pawneensis* Gilmore 1928
Melanosaurus maximus Gilmore 1928

Only a few new taxa have been added to Gilmore's list of fossil anguids. Hecht (1959, pp. 132–134) described *Dimetopisaurus wyomingensis* from the Middle Eocene Bridger Formation sediments at Tabernacle Butte in Wyoming and regarded this species as related to Recent *Ophisaurus*. Estes (1963b, pp. 676–680) described *Paragerrhonotus ricardensis* from the Lower Pliocene Barstow Formation of California and suggested a possible resemblance to the xenosaurs. *Glyptosaurus donohoei* was described by White (1952, pp. 186–189) from the Lower Eocene deposits of the Boysen Reservoir area, Shoshone, Wyoming. *Peltosaurus jepseni* (Gilmore, 1942) was described from the Upper Paleocene Silver Coulee beds of the Polecat Bench Formation, Park County, Wyoming. Gilmore (1938) also described a new species, *Xestops piercei*, from the Lower Eocene Wasatch Formation of Wyoming. *Melanosaurus* has had no additional species described, but Hecht (1959) recognized this genus on the basis of scutes, as well as *Xestops* and *Peltosaurus*, from the Middle Eocene Bridger Formation at Tabernacle Butte. *Peltosaurus floridanus* (Vanzolini, 1952, p. 457) is probably a misplaced *P. granulosus* from the White River Formation, since it is unlike the other Thomas Farm Miocene specimens in preservation, and is indistiguishable from *P. granulosus*, as Estes has noted (1963a, pp. 252–253).

Although the list of new genera and species of North American fossil anguids has not increased appreciably, a number of fossil fragments has been referred to extant genera or species, especially to the genus *Ophisaurus*.

Auffenberg (1955, pp. 133–136) refers fossil vertebrae from the Pleistocene of Florida to two Recent species of *Ophisaurus*, *O. ventralis* and *O. compressus*. His identification rests on neural spine angles formed with the centrum and on ratios of centrum length to width. Holman (1958, p. 278) lists *Ophisaurus ventralis* on his faunal list from the Pleistocene Saber-tooth Cave of Florida. His *Ophisaurus* material consists of two dentaries and three thoracic vertebrae, and his identification rests on measurements of vertebrae adopted from Auffenberg. Etheridge (1960, pp. 46–67; 1961, pp. 179–186) refers vertebrae from the Upper Pliocene and Pleistocene of Kansas and the Pleistocene of Oklahoma to *Ophisaurus attenuatus*, again utilizing Auffenberg's method of identification.

Dentaries from the Upper Cretaceous Lance Formation of eastern Wyoming are compared with Recent *Gerrhonotus* by Estes (1964, pp. 122–125). His main criterion for distinguishing this form from "*Peltosaurus*" *piger*, a more abundant form in the Lance, is tooth structure. McKenna (1960, p. 10) also lists *Gerrhonotus* and *Peltosaurus* in his faunal list of the Lower Eocene of Northwestern Colorado, from identifications provided by Estes. Gazin (1956, p. 12) refers four dentary fragments, two maxillary fragments, and a premaxilla to the family Anguidae from the Upper Paleocene Bison Basin locality of Wyoming. This deposit is of Tiffanian (late Paleocene) age.

Pancelosaurus new genus

Type species of the genus. *Peltosaurus*? *piger* Gilmore 1928

Geological range. Late Cretaceous—Middle Oligocene.

Referred species. *Pancelosaurus piger* (Upper Cretaceous-Paleocene), *P. pawneensis* (Oligocene).

Etymology. Hungarian, *pancél*—armor; Greek, *sauros*—lizard.

Pancelosaurus piger (Gilmore) 1928

Peltosaurus? *piger* Gilmore 1928
Odaxosaurus obliquus Gilmore 1928
Peltosaurus jepseni Gilmore 1942
Peltosaurus piger Estes 1964

Holotype. USNM 10687. The specimen consists of the posterior portion of the right dentary, containing six teeth and spaces for three others.

Type locality. "Peterson's quarry," Lance Creek, Niobrara County, Wyoming.

Horizon. Lance Formation, Upper Cretaceous.

Introduction. Gilmore (1928, p. 316) described a new species, *Peltosaurus*? *piger*, on the basis of two jaw fragments, a right dentary, USNM 10687, and a right maxilla, USNM 10688, both from the Upper Cretaceous Lance Formation of Wyoming. The tentative generic assignment of this new species rested on tooth structure, which according to Gilmore was "remarkably like that of *Peltosaurus granulosus*."

Estes (1964, pp. 119–122) described the parietal and osteoscutes of this lizard, and gave a more detailed description of the maxilla and dentary based on a large number of specimens from the Lance Formation.

Identification of Skeletal Elements

The fossils at the localities from which *Pancelosaurus piger* is known consist of dissociated, often fragmentary individual bones. Practically no two individual skeletal elements articulate with one another; therefore assignment of individual skeletal elements to this genus and species rests on comparative study. The holotype of *P. piger* is a dentary that bears teeth; therefore, the assignment of marginal tooth-bearing bones such as maxillae and premaxillae to the above species is relatively easy on the basis of tooth comparison. Body osteoscutes and skull elements fused with the covering osteoscutes (parietals and frontals) are easily identified as anguid. From the Lance Formation only two anguid lizards are known (Estes, 1964): *Pancelosaurus piger* and a form in which the structure of the teeth and dentaries compares well with *Gerrhonotus*. The former is by far the more abundant of the two. The Lance frontals are not similar to those of the Recent *Gerrhonotus*, and also their size is more consistent with reference to *P. piger*. No other type of anguid frontal is known from the Lance Formation. The situation in the Hell Creek Formation (Bug Creek Anthills local fauna) is essentially the same as in the Lance (Estes, Berberian, and Meszoely, 1969; Sloan and Van Valen, 1965).

An MCZ collection of lower vertebrate remains from the early Paleocene Bison Basin locality (Gazin, 1956) consists mostly of skeletal elements referable to *Pancelosaurus piger;* other lizard remains are extremely rare. This greatly facilitates the assignment of individual bones that do not occur in the Lance or the Bug Creek Anthills to *P. piger,* especially if these elements occur at the same frequency as those elements that can be assigned with certainty to this species.

Bones that are not associated with osteoscutes and do not bear marginal teeth have been assigned to *P. piger* by careful comparison with disarticulated Recent skeletal material and with the same elements of articulated Eocene and Oligocene anguids.

Description and Comparison of Skeletal Elements

Since no significant differences occur among bones of *Pancelosaurus piger* from Lance Formation, Hell Creek Formation,

or Bison Basin localities, a general description is given below.

Dentary (Fig. 10c): Estes (1964, p. 120) describes the dentary as follows: "The dentary is robust; the Meckelian fossa is ventral anteriorly and was evidently covered by the splenial over almost its entire length. The intramandibular septum has a free ventral border, the posterior border of which is notched for the Meckelian cartilage. The anterior inferior alveolar foramen forms a notch on the dental ridge below the sixth or seventh tooth from the rear. The external face of the dentary has a large dorsal notch for the coronoid, extending anteriorly to the level of the second tooth from the rear. The teeth are pleurodont, closely spaced, anteroposteriorly compressed; the maximum number of dentary teeth is nineteen. The shafts of the teeth exclusive of the crown are lingually expanded and bulbous. The crown is relatively small and has an enameloid covering. The most anterior teeth are slightly procumbent and are less lingually expanded than the posterior ones. The tooth bases are subrectangular and the shafts are relatively thick. The tooth apices have horizontal cutting edges that are set at a slight angle to each other, trending anteromedially-posterolaterally, and the crowns are wrinkled lingually and labially."

Comparison. The teeth of *Pancelosaurus piger* resemble most closely those of the fossil *Peltosaurus granulosus*. However, the latter lacks the enameloid dark brown covering of the former. Dark colored enameloid material is also present on the apices of the teeth of *Diploglossus monotropis*, and seems to be independent of tooth preservation. In having a free ventral border to the intramandibular septum, *P. piger* is in agreement with the Recent forms *Diploglossus* and *Gerrhonotus*, but is in strong contrast to *P. granulosus*, in which the ventral border of the septum is mostly fused to the dentary; also, in the latter form the Meckelian fossa is more widely open on the lingual side than in *P. piger*. The anterior extremity of the notch on this septum extends to the third tooth from the back in *P. piger* and to the fifth from the back in *P. granulosus*. The posterior margin of the dentary also presents a different outline from that of *P. granulosus*, indicating that the contact of the dentary with the post-dentary bones was different in the two fossil forms. In this last respect, *P. piger* shows a particular resemblance to *Gerrhonotus* and *Ophisaurus* in the far anterior extent of the angular-surangular notch (cf. Figs. 3b-c, 10c, 17).

Maxilla (Figs. 7b, 9c, 10a-b): Estes (1964, pp. 120–121) describes the maxilla as follows: "The maxilla is robust, and bears thirteen to fifteen teeth like those of the dentary. Externally it is faintly wrinkled by osteodermal scars. The nasal process is relatively low. It rises abruptly behind the naris, rounds off dorsally, and slopes rapidly downward to the posterior tip. There is a slight supradental shelf and a strong palatine process. In dorsal view the posterior half of the bone is strongly expanded, twisted laterally, and bears a deep groove for the jugal. The premaxillary process is bifid, with an external portion fitting into the premaxilla, and a medial vomerine portion."

Comparison. In having a relatively short premaxillary process with a prominent bifid anterior extremity, the maxilla of *Pancelosaurus piger* resembles that of the Recent *Diploglossus* and *Ophisaurus*. This same process is elongate and barely bifurcate in *Gerrhonotus*. Since a premaxillary foramen is present between maxilla and premaxilla in both of the former Recent genera, the above features are indicative of the presence of this foramen in *P. piger*. The oblique ridge dividing the dorsal surface of the supradental shelf into anterior and posterior portions is well developed in all anguids excepting *Gerrhonotus*, in which it has a feeble development. Also, in this latter form the tooth-bearing portion of the maxilla posterior to the facial process

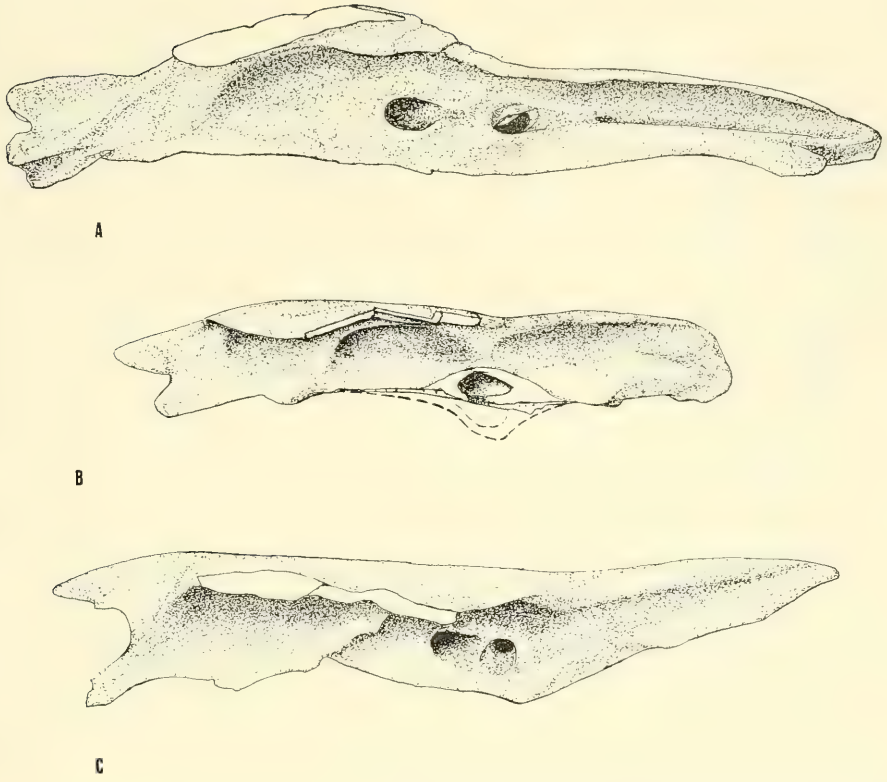

Figure 7. Maxillae, in dorsal view, of recent and fossil anguids. A, *Gerrhonotus liocephalus*, Recent, MCZ 24518; B, *Pancelosaurus piger*, n. gen., UC 49772; C, *Diploglossus hewardii*, Recent, MCZ 7356. Note resemblance between B and C, and the bifid anterior end of B, indicating the possible existence of a premaxillary foramen. Ascending processes of maxillae broken in all to allow view of internal structures. All × 8.

is relatively very long, whereas this same area is very short in *P. piger*. In *Ophisaurus* it has approximately the same proportion as in *P. piger*, while in *Diploglossus* its relative length is in between those of the above forms. The tooth count of 13–15 in *P. piger* is very low for anguids, equalled only by some species of *Diploglossus*. This tooth count is exceeded in all other Recent anguids except *Anguis* and in fossils where a tooth count is available. *Peltosaurus granulosus* and *Melanosaurus maximus* have a maxillary tooth count of 16–17. The low tooth count and the short maxillary ramus posterior to the facial process apparently indicate that *P. piger* was a short-nosed, broad-faced anguid lizard.

Frontal (Figs. 8c, 12a): Frontals distinct with almost straight orbital borders somewhat expanded posteriorly. Osteoscutes fused to underlying bone and sculptured with irregular pits and ridges. Imprint of large frontoparietal scale extending anteriorly less than one-third the total length of frontal. Frontoparietal separated from metopic suture by much smaller mesial interparietal impression. At anterior extremity of frontal, V-shaped incision marks point of overlap by nasal bone. Lateral to V-shaped incision, frontal devoid of osteoscutal crust, indicating position of prefrontal osteoscute. Very small portions of posterolateral corner of frontal also devoid of sculpture.

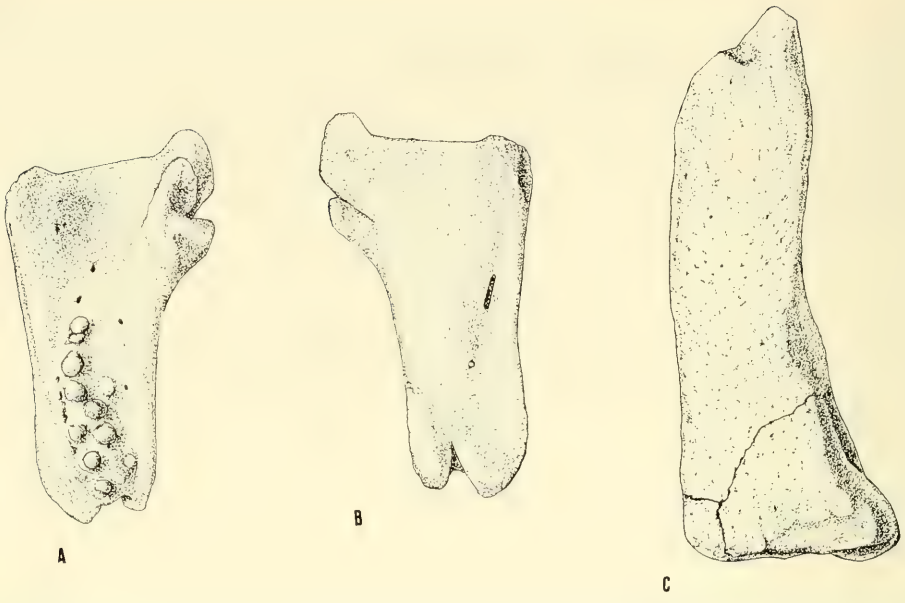

Figure 8. *Pancelosaurus piger*, n. gen. A, left palatine, ventral view, MCZ 3495; B, the same, dorsal view; C, right frontal, dorsal view, UC 61414; A–B, Upper Paleocene Bison Basin deposits, Wyoming; C, Upper Cretaceous Lance Formation, Wyoming. All × 8.

In lateral view frontal displays two deep incisions. Large anterior prefrontal incision occupies over half and smaller prefrontal incision one-third total length of orbital border of frontal bone. The above incisions separated by about one-seventh total length of this bone. Olfactory processes on ventral surface well developed, but separated ventrally.

Comparison. The frontals of *Pancelosaurus piger* resemble closely those of Recent *Diploglossus;* they agree in general outline, in epidermal scalation as indicated by impressions on the osteoscutal surface, in being suturally distinct, and in having nearly identical sculpture on the osteoscutes covering these bones.

In *Pancelosaurus piger,* as well as in *Diploglossus,* the frontoparietal scale impressions are large, and left and right scales are well separated from one another at the midline by the interparietal scale impression. Similar scalation is also found in the fossil *Xestops vagans* and the Recent ophisaurs, *Anguis,* and diploglossines. The sculpture of the osteoscutal surface in *P. piger* is of irregular pits and ridges, in strong contrast to the raised tubercular mounds on the frontals of *X. vagans.*

In *Ophisaurus,* the frontoparietal epidermal impressions are much smaller and more widely separated than in *Pancelosaurus piger;* there is less correspondence in general outline, as well. The entire lateral edges of the *Ophisaurus* frontals are devoid of osteoscutes as a result of the presence of small, loosely-attached osteoscutes covering this area.

Pancelosaurus frontals share only a similar type of dermal sculpture with the fused, emarginate frontals of Recent *Gerrhonotus,* but in some members of *G.* (*Barisia*) the sculptured surface becomes much more pronounced than in any of the other Recent anguids or in *Pancelosaurus.*

The frontals of *Pancelosaurus piger* bear little resemblance to the large Eocene and Oligocene forms *Peltosaurus, Melanosaurus, Arpadosaurus* (n. gen., see p. 136), and *Glyptosaurus.* In *Glyptosaurus* the

osteoscutal crust is broken up into numerous polygonal plates, and in *Arpadosaurus* grooves on the osteoscutal crust indicate an epidermal scalation highly unusual among anguids. In *Melanosaurus* the epidermal scalation is not clear because of weak scale impression on dorsal surfaces of the frontal bone in all fossil specimens referable to this genus. However, the frontal bones are coossified in *Melanosaurus* and also differ in shape from those of *P. piger*. *Peltosaurus* also has coossified frontal bones and exhibits an epidermal scalation in which the two frontoparietal scales are in broad contact on the midline along almost their entire length.

Parietal (Figs. 9e, 16e): Parietal unpaired, with straight frontoparietal suture and gently concave lateral borders. Parietal table longer than wide, with over one-half of dorsal surface covered by osteoscutal crust. Supratemporal processes expanded, slightly exceeding frontoparietal suture in breadth. Faint grooves on osteoscutal crust indicate outline of interparietal, occipital, and parietal epidermal scales. Interparietal scale area a large, posteriorly-directed triangle, containing parietal foramen near apex. Occipital in contact with apex of interparietal, also triangular, but much smaller. Rest of osteoscutal crust occupied by two lateral parietal scale areas. On ventral surface anterior ridges converge posteromedially to form triangle; parietal fossa located at apex of triangle. Parietal fossa an anteriorly-directed oblique pit, located two-thirds of the way back on parietal table. Two small parallel ridges lead from posterior parietal notch to parietal fossa, forming shallow trough. Two posterior ridges follow lateroposterior border of parietal closely and merge with anterior ridges at point somewhat more than one-half the distance from anterior margin.

Comparison. The parietal of *Pancelosaurus piger*, like the frontals, bears the closest resemblance to that of the Recent *Diploglossus*. The sculpture of the osteoscutes fused with the bone resembles that found in the Recent forms and is in strong contrast to the tubercular mounds of *Xestops*, *Peltosaurus*, *Melanosaurus*, *Arpadosaurus*, and *Glyptosaurus*. The epidermal scale impressions on the osteoscutal surface also resemble those of the Recent forms. The interparietal impression is wide and large, whereas that of the occipital is very small. In *Peltosaurus granulosus* and in *Melanosaurus maximus* these two impressions are nearly the same size, and the interparietal impression is much narrower than in the Recent forms and *Pancelosaurus piger*. The osteoscutal crust covers over half of the parietal table in *P. piger*, as it does in *Diploglossus* and *Ophisaurus;* in *Gerrhonotus* less than half of the parietal table is covered by osteoscutes. In *Gerrhonotus*, this area is also much more elongated, and the supratemporal processes are less divergent than in *P. piger*. On the ventral surface a trough leads to the parietal fossa between two parallel ridges, which are the posterior extensions of the anterior ridges. This trough has the same relative length in *Diploglossus* and *P. piger*. The same trough is much shorter in *Ophisaurus* because of the very posterior location of the parietal fossa. In *G. liocephalus* there is no trough because the two anterior ridges join to form a single posterior median ridge. In *Peltosaurus granulosus* the situation is similar to that in *Pancelosaurus* and *Diploglossus*, but the proportions are different as a result of widening of the parietal table in the former.

Palatine (Fig. 8a, b): Palatine a spatulate bone with expanded anterior end; anterior margin of bone nearly straight. Ventral surface of bone bears a patch of tubercular teeth; tooth patch is two teeth wide and extends from posterior extremity to a little more than one-half entire length of bone. Point where the teeth end marks the beginning of broad depression that forms internal choana. On both sides of choanal depression edges of palatines

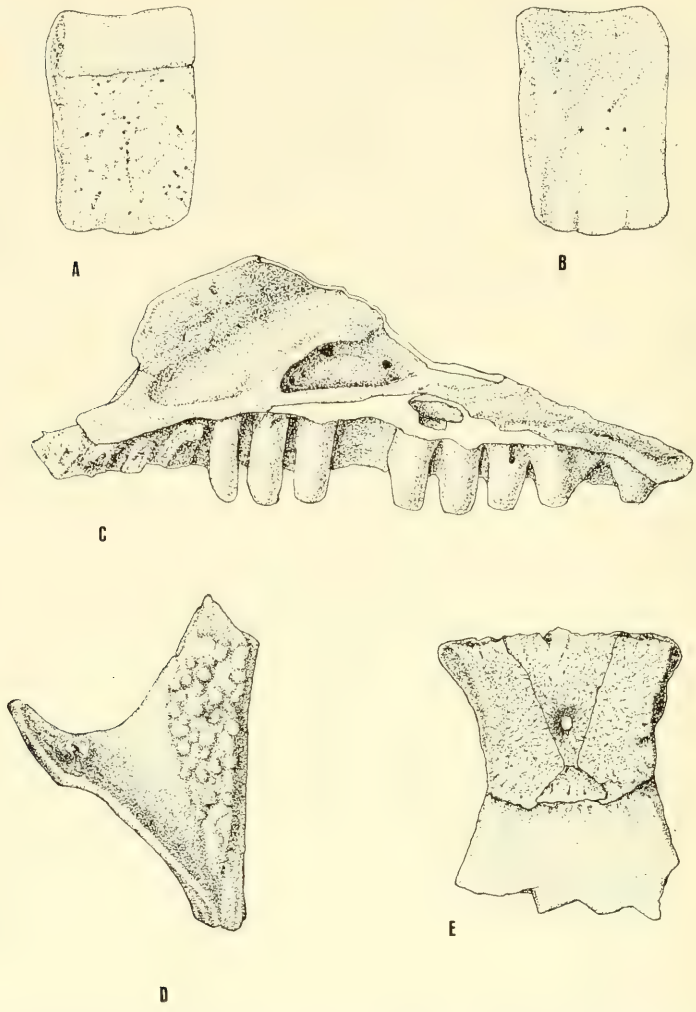

Figure 9. *Pancelosaurus piger*, n. gen. A, body osteoscute, dorsal view; UC 61414; B, the same, ventral view; C, maxilla in lingual view, UC 49772; D, right pterygoid, ventral view, MCZ 3497; E, parietal in dorsal view, MCZ 3498. A–B, Upper Cretaceous Hell Creek Formation, Montana; C, Upper Cretaceous Lance Formation, Wyoming; D, Upper Paleocene Bison Basin deposits, Wyoming. A–D × 8, E × 4.

curled ventrad; mesial edge bears small vomerine process, lateral edge with larger maxillary process. Latter process exhibits oval articular surface, which in Recent anguids is overlapped ventrally by maxilla. Oval articular surface bears anterior notch for the exit of superior alveolar nerve, which in Recent anguids enters maxilla at this point. Infraorbital canal completely surrounded by palatine bone as in all anguids; however, in majority of fossils this process damaged, giving appearance of notch to infraorbital foramen.

Comparison. In having a toothed palatine bone, *Pancelosaurus piger* agrees among the Recent forms only with *Ophisaurus*, in all species of which this bone bears teeth. Among the fossil forms toothed palatines appear to be the rule. *Arpadosaurus*, *Melanosaurus*, and *Peltosaurus* all

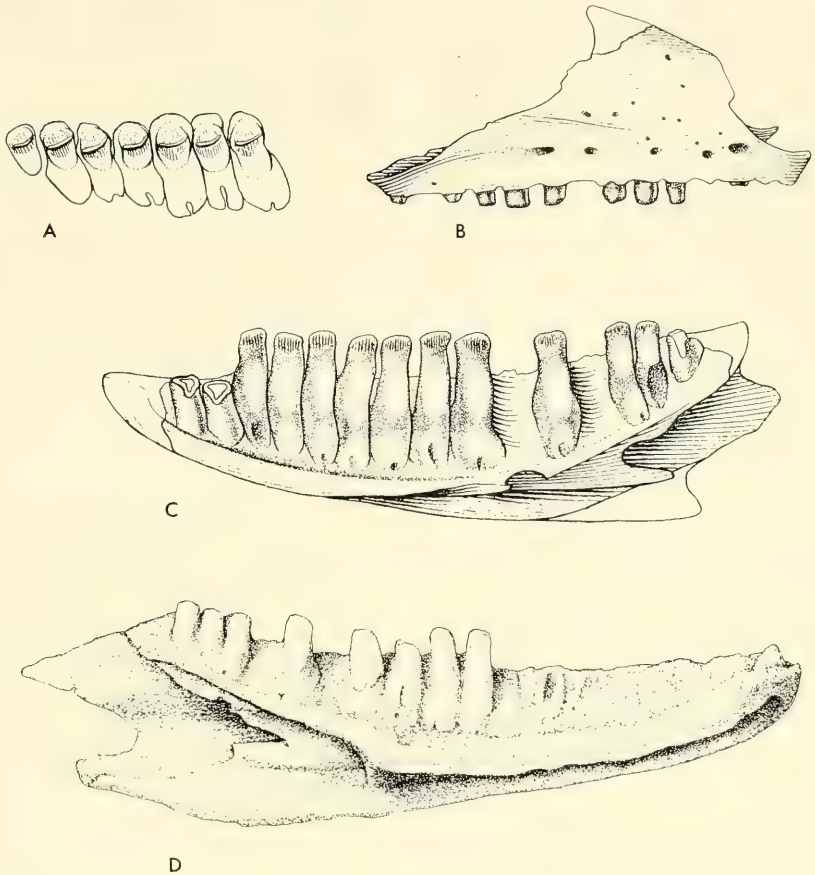

Figure 10. *Pancelosaurus piger*, n. gen. A, UC 47756, occlusal outline of seven posterior left dentary teeth; B, UC 49772, right maxilla, labial view; C, UC 47756, right dentary, lingual view; D, *Peltosaurus granulosus*, KU 1282, lingual view, left dentary. A–C from Estes, 1964, Upper Cretaceous Lance Formation, Wyoming; D, Oligocene, White River Formation, Colorado. All × 6.

bear teeth on the palatine; in other fossil genera the palatine bone is not known.

The general outline of palatine bones is similar in anguids, but in *Diploglossus* the choanal depressions extend posteriad more than half the entire length of this bone, while in the other Recent forms, as well as in *Pancelosaurus piger*, the choanal depression comprises less than one-half the total length of the palatine bone.

The infraorbital canal, in common with that of most anguimorphs, is a foramen rather than a notch on the maxillary process of the palatine. Anguids also usually have a relatively straight anterior margin to this bone, whereas in non-anguids the anterior margin of this same bone is often strongly slanted. A foramen on the maxillary process of the palatine was observed in all Recent forms, and in the fossil *Pancelosaurus piger*, *Peltosaurus granulosus*, and *Arpadosaurus* (in the other fossils this area is not observable).

Pterygoid (Fig. 9d): Pterygoids with patch of tubercular teeth along ventromedial margin. Tooth patch four to five teeth wide and extending to anterior extremity of pterygoid, thus forming con-

tinuous palatal tooth patches with palatines. Tooth-bearing area triangular, with lateral apex bearing anteriorly-directed ectopterygoid process. Dorsal surface of bone smooth with deep, triangular, anterolateral ectopterygoid incision.

Comparison. In having teeth, the pterygoids of *Pancelosaurus piger* resemble those of the Recent ophisaurs and members of the subgenus *Gerrhonotus*. Pterygoid teeth as well as palatine teeth are present in every fossil anguid in which this bone is known: *Glyptosaurus, Peltosaurus, Xestops* and *Melanosaurus*.

In *Pancelosaurus, Ophisaurus,* and *Anguis* the palatine process of the pterygoid extends well in front of the maxillary process; in other anguids the anterior extremities of the above processes are nearly in line.

Premaxilla (Fig. 11): Premaxilla an unpaired, anchor-shaped bone in anterior view, with broad nasal spine. Nasal spine constricted at its base. Rostral body relatively wide, with its anterior margin gently arched in dorsal view, lateral maxillary processes well developed. Maxillary processes bearing deep dorsal triangular incision for maxillae. Near base of nasal spine three posterolateral foramina present on each side.

Prominent medial suture present on lingual surface of nasal spine extending to posterior extremity of palatine process. Incisive process broken in all examined specimens. Premaxillary tooth count nine. Teeth essentially as described for other jaw elements. Large unpaired foramen present posterior to medial tooth, becoming paired at short distance from its origin.

Comparison. The rostral body of the premaxilla of *Pancelosaurus piger* is similar to that of the Recent *Diploglossus*. In both, the maxillary processes are elongated in dorsal view, and the outline of the anterior margin of the rostral body is gently arched. In Recent *Gerrhonotus* the rostral body is much shorter as a result of the shorter maxillary processes; hence there is less participation by this bone in the formation of the external nares. In *Ophisaurus* the anterior border of the rostral body is not arched; the left and right sides meet at a strong angle to one another and present an inverted V in dorsal view. In *P. piger,* as in *Ophisaurus* and *Diploglossus,* there is a notch or constriction at the base of the nasal spine; in *Gerrhonotus* the base of the nasal spine is not constricted, but the spine emerges from the rostral body gradually, narrowing in a dorsoposterior direction. The rostral body is short and presents the same foreshortened triangular shape in *Melanosaurus* and *Peltosaurus* as in *Gerrhonotus*.

The palatine processes are not preserved in any *Pancelosaurus* specimens, and hence it cannot be determined with certainty if premaxillary foramina were present as in Recent *Ophisaurus, Diploglossus,* and *Anguis*. As indicated above, however, it is very possible that they were present.

Osteoscutes (Fig. 9a, b): Lateral body osteoscutes rectangular and sculptured with irregular pits and ridges. Smooth gliding surface occupies from one-fourth to almost one-half entire length of osteoscute. Prominent smooth oblique surfaces along lateral edges, one ventrally and the other dorsally located, indicate high degree of lateral overlap between adjacent osteoscutes. No evidence of lateral suturing. No keel present on any of the several hundred scutes so far discovered.

Middorsal body osteoscutes fan-shaped, unkeeled, and somewhat expanded posteriad. Extent of area occupied by the gliding surface is variable as above. Along both dorsolateral edges middorsal scutes bear smooth oblique surfaces indicating overlap on both sides by adjacent scutes.

Comparison. Osteoscutes of *Pancelosaurus piger* bear the closest resemblance to those of Recent *Gerrhonotus* and *Ophisaurus,* agreeing with the latter genera in the following characteristics:

(1) Sculpture consisting of pits and ridges.

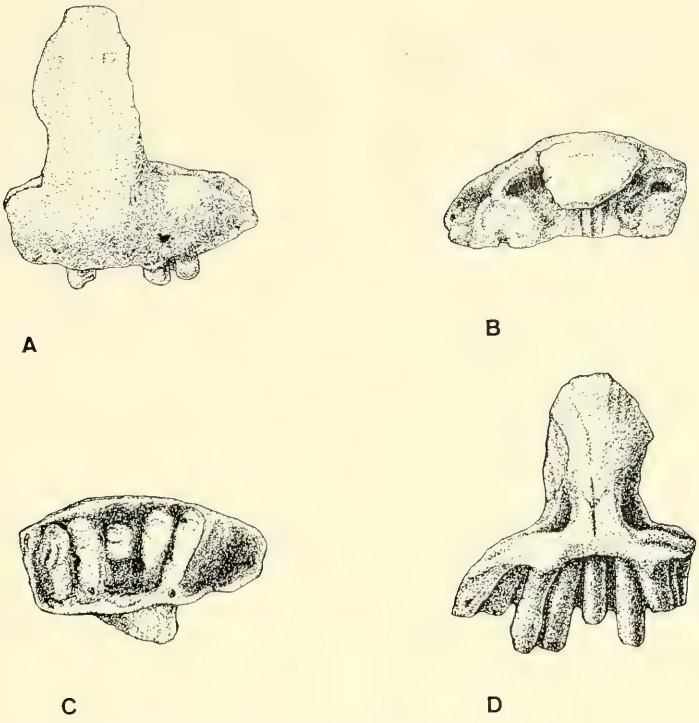

Figure 11. *Pancelosaurus piger*, n. gen. MCZ 3690, premaxilla, A, anterior, B, dorsal, C, ventral, and D, posterior views. Bison Basin deposits, late Paleocene, Wyoming; × 8.

(2) Gliding surface in the shape of an anterior transverse band.

(3) Osteoscutes with rectangular outline.

(4) Prominent beveled lateral margins.

(5) No evidence of lateral suturing of osteoscutes to one another.

In all of these characters except number 1, osteoscutes of *Peltosaurus granulosus* agree with those of *P. piger*, but the former have a strikingly different sculpture, consisting of raised tubercular mounds.

Xestops vagans has sculpture of the osteoscutes identical to that of *Peltosaurus granulosus* and also agrees in most of the above points with *Pancelosaurus piger*, but in *X. vagans* the jagged edges of the osteoscutes are indicative of some lateral suturing; nevertheless they are beveled as well. In *X. vagans* the osteoscutes are also more robust than in *P. piger* and are keeled.

Osteoscutes of the large Eocene and Oligocene fossils *Melanosaurus*, *Arpadosaurus*, and *Glyptosaurus* are also rectangular, and the gliding surface is arranged in the shape of a transverse band. Sculpture of the osteoscutes is the same in these forms as in *Xestops* and *Peltosaurus*, but in the former genera the tubercular mounds are often arranged in concentric rectangles. In *Glyptosaurus*, *Melanosaurus*, and *Arpadosaurus* a number of the osteoscutes bear keels. There is little lateral overlap in these forms between osteoscutes, and the lateral margins bear jagged edges indicative of lateral suturing.

The general appearance of the osteoscutes of *Pancelosaurus piger* is least similar to that of the Recent *Diploglossus*. In *Diploglossus* the osteoscutes are round

or ovoid and have a gliding surface with a concave posterior border with a prominent posterior peak. Sculpture of the osteoscutes is similar in *P. piger* and in *Diploglossus.*

Vertebrae: Thoracic vertebrae procoelous, robust, relatively short, and triangular in ventral view. Anterolateral corners of triangle strongly expanded laterally and bearing articular surfaces for ribs; rib articular surfaces dorsoventrally elongated. Ventrally, on both sides of subcentral keel, centrum bears lateral depressions; depressions extending along ventrolateral margin of centrum from rib bearers to condylar ball; condylar ball wide but with little ventral exposure. Neural arches moderately low, with zygapophyses ranging from nearly circular to subcircular; feebly-developed zygosphenes and zygantra present; prezygapophyses tilted at sharp angle upward and inward. Neural canal relatively large, exceeding height of centrum in anterior view, and breadth equal to cotylar depression; cotyle deeply excavated. Relative length of individual centra highly variable in available fossil sample, presumably corresponding to regional variations observable in Recent anguids.

Comparison. Trunk vertebrae of *Pancelosaurus piger* are not flattened ventrally as in the limbless *Ophisaurus, Anguis,* or *Ophiodes;* the midventral area of the centrum is convex as in the limbed forms *Gerrhonotus, Abronia,* and *Diploglossus. Pancelosaurus* was thus probably a limbed form. The vertebrae of *P. piger* are unique among anguids in having zygosphenes and zygantra. In having a wide condyle with little ventral exposure the vertebrae of *P. piger* resemble those of *Diploglossus.* Further comparisons are difficult to make as a result of similarity between trunk vertebrae of Recent limbed forms. There is also a high degree of regional variation in these forms along the vertebral column, which affects the shape of the individual vertebrae. In general, trunk vertebrae from the anterior part of the vertebral column are shorter and more triangular in outline.

Vertebrae of the large fossil forms such as *Melanosaurus* and *Glyptosaurus* are also triangular in ventral outline, but here the centrum is relatively shorter and more expanded anterolaterally than in *Pancelosaurus piger.* The condyle is also large in *Melanosaurus* and *Glyptosaurus* and dorsoventrally flattened, exceeding in breadth the centrum at the point where these two structures come in contact.

Discussion. Gilmore (1928, p. 126) provisionally referred a dentary and a maxilla from the Upper Cretaceous Lance Formation to the genus *Peltosaurus,* calling the new species *P.? piger.* McDowell and Bogert (1954, p. 133) not only questioned the generic assignment of this lizard, but considered it probably not anguid. Estes (1964, pp. 119–122) reinstated it in the Anguidae and referred it with more certainty to the genus *Peltosaurus.* However, at that time a number of the diagnostic cranial elements of this lizard were not known. Now that most of the skull bones are known, it appears certain that this form is not referable to the genus *Peltosaurus;* it is here placed in a new genus, *Pancelosaurus. Pancelosaurus piger* differs in a great number of characters from *Peltosaurus granulosus,* the genotypic species. (1) *Pancelosaurus piger* has a sculpture consisting of irregularly-arranged pits and ridges on its body osteoscutes as well as on the osteoscutes fused with the cranial elements, in strong contrast with the raised tubercular sculpture of *Peltosaurus granulosus.* (2) The epidermal scale impressions on the frontals and parietals are also markedly different. On the frontal bones of *P. piger* the frontoparietals are widely separated, whereas in *P. granulosus* the same two scales are in broad contact. On the parietal bone in *P. piger* the interparietal impression is very large, whereas the occipital is small; the two impressions are nearly the same in *P. granulosus.* (3) The frontals are paired in the Cretaceous form,

whereas the same bones are fused in *P. granulosus*. (4) The rostral body of the premaxilla in the former is much more extended laterally than in the latter. (5) While in tooth structure the two forms are not unlike, the morphology of the structures in the Meckelian fossa differs markedly in the two lizards. The fossa is widely open lingually in *Peltosaurus*, and the intramandibular septum is placed well forward, whereas in *P. piger* this same septum is close to the posterior margin of the dentary, and the Meckelian fossa is less open here. In *Peltosaurus* the ventral border of the septum is almost completely fused with the rest of the dentary; in *P. piger* this same septum has a free ventral border. There are also some other, minor, differences between individual skeletal elements of the two genera as noted in the comparisons.

These same skeletal comparisons indicate that not only is *Pancelosaurus piger* not referable to the genus *Peltosaurus*, but in a number of its known characters this early anguid resembles the Recent forms more than it does most of the Eocene and Oligocene fossil anguids.

In the morphology of a number of individual cranial elements—frontal, parietal, maxilla, and premaxilla—*Pancelosaurus piger* resembles most closely the Recent *Diploglossus*, but differs from this Recent form in structure of the osteoscutes and in having toothed palatal elements. The ophisaurs differ from the diploglossines in these same respects, and it is with *Ophisaurus* that *P. piger* has the greatest number of fundamental characters in common: (1) Paired frontals. (2) Same type of rectangular body osteoscutes; sculpture of cranial and body osteoscutes similar. (3) Palatines and pterygoids both toothed (vomers unknown). (4) Frontoparietal scales separated at the midline, the separation of these scales greater in *Ophisaurus* than in *P. piger*. (5) Palatine process of pterygoid in advance of maxillary process. Confirmation of the presence (suggested below) of a premaxillary foramen in *P. piger* would be of great importance, but since this fossil is known only from isolated bones, only suggestions can be made. The rostral body of the premaxilla of *Pancelosaurus piger* has an elongated maxillary process. The premaxillary process of the maxilla is short and strongly forked, and a septomaxillary fossa is present internal to the facial process. All these features contrast with the situation in *Gerrhonotus*, which lacks a premaxillary foramen, and agree with *Diploglossus* and *Ophisaurus*, in which such a foramen occurs, suggesting that it was also present in *P. piger*. However, the lingual margin of the premaxillae of *P. piger* is damaged in all specimens, and it is in this area that the delicate processes extend toward the inner prong of the anterior forked end of the maxilla, forming a premaxillary foramen.

Some of the characters shared by *Pancelosaurus piger* and the extant ophisaurs, such as paired frontals and toothed palatal elements, are without doubt primitive for anguids as well as for other lizards. Separation of the left and right frontoparietal scales on the midline also appears to be primitive for anguids, as suggested by the presence of such a condition in the overwhelming majority of extant anguids, as well as in another early anguid fossil, the Eocene *Xestops vagans*. In the probable possession of a premaxillary foramen and in having rectangular osteoscutes, *Pancelosaurus piger* exhibits an intermediate position (similar to *Ophisaurus*) between *Gerrhonotus* and *Diploglossus*. Resemblances of individual cranial elements between *Diploglossus* and the fossil *P. piger* are much greater than resemblances between *Ophisaurus* and *Diploglossus*. McDowell and Bogert (1954, p. 117) made the statement that "the Galliwasps (diploglossines) appear to be the most primitive of the Anguinomorpha"; this statement is supported by this study in that diploglossines show the greatest resemblance in a number of cranial elements to *Pancelo-*

saurus piger. However, the osteoscutes of diploglossines are radically different from those of *P. piger*, which in this feature agree with the extant ophisaurs and *Gerrhonotus*.

The occurrence of *Gerrhonotus*-like and *Ophisaurus*-like osteoscutes in *Pancelosaurus piger* may indicate one of two possibilities: (1) That *P. piger* is already somewhat specialized toward the line leading to these Recent forms and perhaps also to the large Eocene and Oligocene fossil forms, and that diploglossines represent an early divergent line from all other known anguids. (2) A less likely possibility in the present state of our knowledge is that the diploglossine scute was derived from the *Pancelosaurus* type of osteoscute. I consider the first alternative the simplest and more probable, and refer *Pancelosaursus* to the Anguinae.

Among the large Eocene-Oligocene anguids, *Pancelosaurus piger* shows the greatest number of characters in common with *Xestops vagans*. These two forms agree (1) in the arrangement of frontoparietal scale impressions on the frontals, (2) in having paired frontals, and (3) in having toothed palatines. The osteoscutes are also somewhat similar in regard to general shape and in their beveled lateral edges, but the osteoscutes of *X. vagans* also show indications of lateral suturing. The osteoscutes of the two fossils differ in sculpture as well, and those of *X. vagans* bear keels.

The size of the isolated bones of *Pancelosaurus piger* suggests a lizard with a skull about 30 mm long. The vertebrae of *P. piger*, with their raised, rounded midventral area suggest a limbed rather than a limbless anguid (in the latter the centrum is markedly flattened ventrally), and this is substantiated by the presence of numerous limb bone fragments at the Bison Basin locality that are almost certainly referable to *P. piger*.

The type specimen (PU No. 14565) of *Peltosaurus jepseni* (Gilmore, 1942) now consists of only a posterior portion of the parietal bone and a body osteoscute. The maxilla associated with the type material and described by Gilmore (1942, p. 162) is now lost or misplaced. The osteoscutal crust covering the type parietals bears a sculpture consisting of low irregular ridges and pits and identical to that of *Pancelosaurus piger*, but in strong contrast to the granular ornamentation of *Peltosaurus granulosus* and *P. abbottii*. The small but wide occipital scale impression on the osteoscutal crust of *P. jepseni* is also in agreement with that of *P. piger*, but, again, differs from the elongate, relatively narrow, occipital scale impression of the peltosaurs. The osteoscutes are identical with those found in *P. piger*.

The type material of *Peltosaurus jepseni* is now supplemented by a nearly complete parietal, toothed pterygoids, and numerous jaw elements from the type locality. All the known skeletal elements of this form resemble these same elements of *Pancelosaurus piger*, and there is little doubt that the generic affinities of "*Peltosaurus jepseni*" are with *Pancelosaurus*. Even though the lizard remains referred to "*Peltosaurus jepseni*," as well as those described above from the Bison Basin sediments in Wyoming, are of Tiffanian (late Paleocene) age, there is no indication of specific distinction in the morphology of these remains from those of the late Cretaceous *Pancelosaurus piger*. *Peltosaurus jepseni* is therefore included here in the synonymy of *Pancelosaurus piger*.

Summary. (1) The earliest known fossil anguid is from the Upper Cretaceous Lance Formation and was questionably referred by Gilmore (1928) to the genus *Peltosaurus*. The Cretaceous form has little in common with the genotype from the Oligocene, and is here placed in a new genus *Pancelosaurus*.

(2) *Pancelosaurus piger* shows greater resemblances to Recent anguids than to the large Eocene-Oligocene forms in size

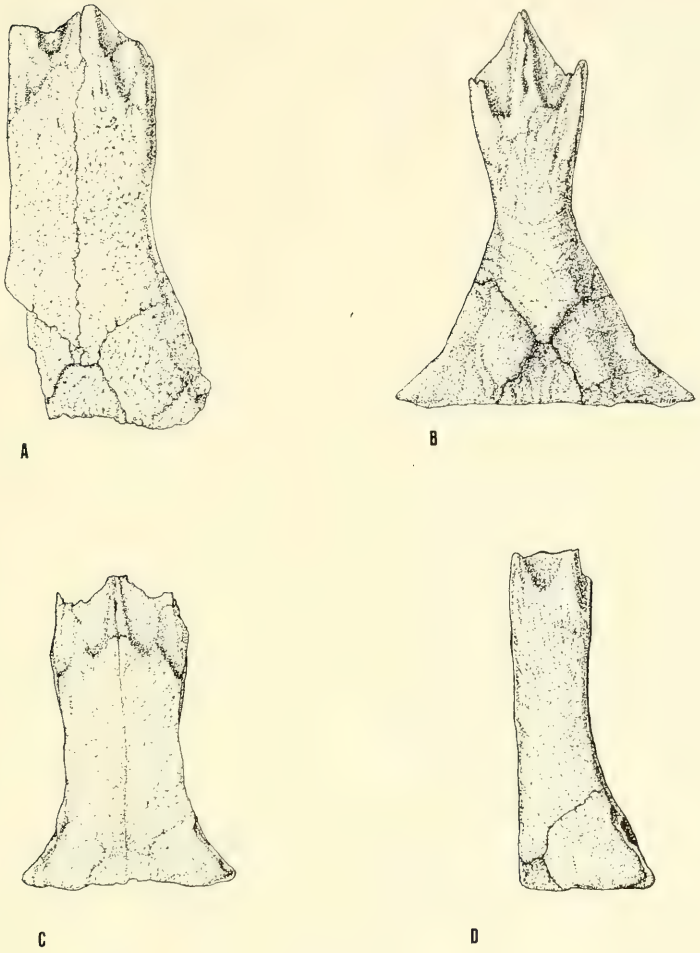

Figure 12. Frontals of recent and fossil anguids in dorsal view. A, *Pancelosaurus piger*, n. gen., (Bison Basin), MCZ 3496; B, *Gerrhonotus liocephalus*, Recent, MCZ 24518; C, *Diploglossus hewardii*, Recent, MCZ 7356; D, *P. piger* (Hell Creek Formation, Montana), MCZ 3499. Note close resemblance between A and C. All × 4.

and arrangement of epidermal scales and in osteoscutal sculpture.

(3) The diploglossines exhibit a number of apparently primitive cranial characters, as indicated by the close resemblance between their individual skeletal elements and those of *Pancelosaurus piger*.

(4) The osteoscutes of *Pancelosaurus piger* are essentially the same as those found in *Gerrhonotus* and *Ophisaurus*, and unlike those of *Diploglossus*.

(5) *Pancelosaurus piger* exhibits the greatest number of fundamental characters in common with *Anguis* and the ophisaurs, and is referred to the subfamily Anguinae.

(6) Among the large early Tertiary anguids, *Pancelosaurus piger* resembles *Xestops vagans* most closely.

Pancelosaurus pawneensis (Gilmore 1928)

Xestops? pawneensis Gilmore 1928

Holotype. KU 1281. Gilmore based this species on the "median section of an articulated skull, with median part of attached

right ramus." The box bearing the above museum number now contains only a mesial portion of the right mandible, a small portion of the left maxilla, and fragments of the posterior portion of the right frontal.

Diagnosis. Similar in known characters and size to *Pancelosaurus piger,* differing from the latter in having recurved teeth with pointed apices that lack enameloid covering or striations.

Type locality. Sect. 28, T 11 N, R 53 W, 30 miles N of Sterling, Logan Co., Colorado.

Horizon. White River Formation (Cedar Creek beds), Middle Oligocene.

Original description. Gilmore (1928, p. 150) described this specimen as follows: "The teeth are closely placed subcylindric, with upper and lower teeth indistinguishable. In the maxilla eight and one-half teeth occupy a space of 5 millimeters. In size and lack of surface ornamentation these teeth bear a striking resemblance to those of *Exostinus serratus* found in this same region, differing chiefly in their more pointed apices.

"On account of the frontal bone being coossified with the overlying scutes it can not be determined whether the frontals were distinct or not. The granular surface ornamentation is similar to that in *X. vagans,* and the frontoparietal scutes are separate on the mid line as in that species. The post- and prefrontals are perhaps less widely separated above the orbits in this new species. Between the orbits the frontal bone has a width of 5 millimeters.

"The orbits are large, subcircular in outline; nasals distinct. That portion of the palate still preserved, consisting of articulated palatines and vomers, bears a strikingly close resemblance to the palatal region of *Gerrhonotus,* and apparently indicates its anguid relationship. The vomers are in close apposition in front, separated by a fissure posteriorly, the anterior ends slightly excavated on their inferior surfaces. Palatines descending from the plane of the vomers; vomerine and maxillary processes subequal in size. Palatine foramen of good size. The presence of a single small body osteoderm with the skull is all that we know of the dermal covering. Its external surface is sparsely pitted, and it shows the usually smooth overlap surface at one end."

Redescription of the remaining type material. The frontal fragment, consisting of the right posterior corner of this bone, displays a sculpture pattern consisting of irregularly arranged pits and ridges, and not a "granular. . .ornamentation," as Gilmore described it. On the osteoscutal crust the outline of a large frontoparietal scale is imprinted. The postfrontal incision reaches to almost the anterior extremity of the above scale imprint. The lateral corner of the frontal fragment is devoid of osteoscutal crust.

The right mandibular fragment contains four teeth, the crowns of which are badly damaged. On the lingual surface the anterior inferior alveolar foramen is bordered by the dentary above and the splenial below. The anterior mylohyoid foramen is surrounded by the splenial alone. The anterior portion of the preserved splenial bone is ventral in position.

The maxillary fragment contains eight complete teeth and one fragmentary one. Three of the teeth are small and are apparently replacement teeth just moving into position. The crowns of the larger teeth are well preserved, and are unstriated with pointed recurved transparent apices. The apices are directed posterolingually. The shafts of the teeth are also slightly inclined posteriad. The facial process of the maxilla is not preserved, but the dorsal surface of the dental shelf bears a channel leading to the infraorbital foramen.

The fragments of the type specimen and Gilmore's original description are beautifully supplemented by two specimens from Round-top, Dawes Co., Nebraska (Lower Brule Formation, Middle Oligocene), FMNH P27236 and P27235, which

Table 1. Anguid Subfamilies and Referred Genera of Various Authors Discussed in text.

Cope 1900	McDowell & Bogert 1954	Hoffstetter 1962	This Paper
Anguinae	Anguinae	Anguinae	Anguinae
Anguis	*Anguis*	*Anguis*	*Anguis*
Ophiodes		*Celestus*	*Ophisaurus*
	Gerrhonotinae	*Diploglossus*	*Pancelosaurus*
Ophisaurinae		*Ophiodes*	
	Abronia	*Sauresia*	Gerrhonotinae
Dopasia	*Coloptychon*	*Wetmorena*	
Hyalosaurus	*Gerrhonotus*		*Abronia*
Ophiodes	(including	Gerrhonotinae	*Coloptychon*
Ophisaurus	*Barisia* and		*Gerrhonotus*
Pseudopus	*Elgaria*)	*Abronia*	(including
	Ophisaurus	*Coloptychon*	*Barisia* and
Gerrhonotinae	(including	*Gerrhonotus*	*Elgaria*)
	Dopasia,	(including	*Paragerrhonotus*
Barisia	*Hyalosaurus*,	*Barisia* and	
Gerrhonotus	and *Pseudopus*)	*Elgaria*)	Diploglossinae
(including	*Placosauriops*	*Glyptosaurus*	
some species	*Placosauroides*	*Melanosaurus*	*Diploglossus*
later referred		*Ophipseudopus*	(including
to *Abronia*)	Diploglossinae	*Ophisauriscus*	*Celestus* and
		Ophisaurus	*Sauresia*)
Mesaspis	*Celestus*	*Parapseudopus*	*Ophiodes*
	Diploglossus	*Peltosaurus*	*Wetmorena*
Diploglossinae	*Ophiodes*	*Placosauriops*	
	Sauresia	*Placosauroides*	Glyptosaurinae
Celestus	*Wetmorena*	*Placosaurus*	
Diploglossus	*Xestops*	*Xestops*	*Arpadosaurus*
Microlepis			*Glyptosaurus*
Onida	Glyptosaurinae		*Melanosaurus*
Panolopus	*Glyptosaurus*		*Paraxestops*
Sauresia	*Placosaurus*		*Peltosaurus*
	Placotherium		*Placosauriops*
			Placosauroides
			Placosaurus
			Xestops

agree with the above description and the remaining type fragments in every detail.

FMNH P27236 (Pl. 1). A skull with mandibles and with most of its parts preserved anterior to the parietal suture. The snout is slightly damaged, and the premaxilla is missing.

Description. The frontals are paired, and the osteoscutal crust on the dorsal surface is sculptured with irregular pits and ridges. The right frontoparietal scale impression does not reach the metopic suture, but is separated from it by a small interparietal impression. That portion of the left frontal that bears this same scale impression is not preserved. The nasal bones are distinct. The prefrontal bone is present and separated from the postfrontal incision. The maxilla has a well-developed facial process. Posterior to this process the maxilla is twisted labially.

The maxilla is nearly complete, with only its most anterior extremity missing. Spaces and preserved teeth indicate a tooth count of 13–14. The teeth are essentially as described for the holotype. In the labial contact between dentary and postdentary bones the surangular is well in advance of

Plate 1. *Pancelosaurus pawneensis*, n. gen., FMNH P27236. Top: Dorsal surface of skull, showing frontals; anterior to the right. Bottom: Left side of the same showing maxilla and mandible. Note pointed teeth. Both × 4. Middle Oligocene, Brule Formation, Nebraska.

the dentary process of the coronoid bone. The preserved portion of the dentary bears seven teeth and spaces for three.

FMNH P27235. The skull of an anguid lizard somewhat smaller than the above, with most of its preserved parts anterior to the frontoparietal suture. The premaxilla is missing, as in the previous specimen, but the palate is here exposed with vomers and palatines visible.

Description. The frontals are the same as described for the previous specimen. Anterior to the frontal bones on the right side a large prefrontal is present, and it was apparently in contact with the left prefrontal scute at the midline. The facial process of the maxilla is not in contact with the frontal bone. The palatines bear a patch of tubercular teeth, but no vomerine teeth are present. The tooth count as indicated by spaces and complete teeth is 13–14 for the maxilla.

Discussion. The type of sculpture on the cranial osteoscutes and the small size of this Oligocene anguid relate it to *Pancelosaurus piger,* rather than to the Eocene *Xestops* as Gilmore (1928) believed. It also differs from *Xestops vagans* in having pointed teeth. Its other known character-states, excepting teeth, are also in agreement with *P. piger* and include (1) unfused frontal bones, with left and right frontoparietal scales separated at the midline, (2) toothed palatines, (3) maxillary tooth count of about 13–14, (4) deep anterior incision on the frontal bone for the nasal, (5) general morphology of the individual cranial elements. The teeth are strikingly different in the two species: blunt and with striated crowns in *P. piger,* unstriated with pointed apices in *P. pawneensis,* indicating the specific distinctness of the latter.

It is interesting that *Pancelosaurus pawneensis* exhibits a labial contact between dentary and postdentary bones similar to that found in modern anguines, and distinct from that shown by its contemporaries *Peltosaurus* and *Glyptosaurus,* or Eocene *Glyptosaurus, Melanosaurus,* and *Xestops.* In *P. piger* the dentary is disarticulated in all known Cretaceous specimens, but the dentary shape indicates that surangular and coronoid were approximately in line as in the glyptosaurines (MCZ 3688, 3689; Hell Creek Formation, Montana). This condition is confirmed by articulated late Paleocene specimens of *P. piger* (specimens formerly referred to *Peltosaurus jepseni;* USNM 16880, Montana and PU 17148, Wyoming). In this feature *P. pawneensis* is specialized toward the Recent anguines.

Xestops Cope 1873

Type species of the genus. Xestops vagans (Marsh 1872).

Geological range. The genus is only known with certainty from the Middle Eocene of North America.

Referred species. Only a single species, *X. vagans,* is recognized here (see below).

Xestops vagans (Marsh 1872)

Oreosaurus vagans Marsh 1872
Dimetopisaurus wyomingensis Hecht 1959

Holotype. YPM 541. The type material consists of the following disarticulated skeletal elements: frontals; three lower jaw fragments, two representing the major posterior portions of left and right dentaries, latter with portions of coronoid, surangular and splenial attached, the third fragment probably representing the anterior portion of the above right jaw fragment; a small portion of the right maxilla; pterygoid; numerous dermal body scutes and unidentified bone fragments. Since the type material consists of numerous disarticulated elements, the frontals are designated here as the lectotype (Fig. 13, a-b).

Horizon. Bridger Formation (Horizon B), Middle Eocene.

Type locality. Grizzly Buttes, Uinta County, Wyoming.

Revised description. The right and left frontals are suturally distinct. The left

Table II. Holotypes of North American Anguid Fossils Examined.

Dimetopisaurus wyomingensis Hecht 1959, AMNH 3819

Glyptosaurus sylvestris Marsh 1871, USNM 16523
G. nodosus Marsh 1871, USNM 16520
G. princeps Marsh 1872, USNM 16539
G. rugosus Marsh 1872, USNM 16526
G. sphenodon Marsh 1872, USNM 16524
G. tuberculatus Douglass 1903, CM 707
G. montanus Douglass 1908, CM 1050
G. giganteus Gilmore 1928, CM 1471
G. hillsi Gilmore 1928, USNM 6004
G. donohoei White 1952, USNM 18317

Melanosaurus maximus Gilmore 1928, AMNH 5168*

Odaxosaurus obliquus Gilmore 1928, USNM 10751 (synonym of *Pancelosaurus piger*)

Peltosaurus granulosus Cope 1873, AMNH 1610
P. abbottii, Gilmore 1928, FMNH 12861
"P." piger Gilmore 1928, USNM 10687 (*Pancelosaurus*, n. gen., see below)
P. jepseni Gilmore 1942, PU 14565*

Xestops vagans Marsh 1872, USNM 16532
X. gracilis Marsh 1872, USNM 16529
X. lentus Marsh 1872, USNM 16531
X. microdus Marsh 1872, USNM 16528
X. minutus Marsh 1872, USNM 16530*
X.? pawneensis Gilmore 1928, KU 1281*
X.? piercei Gilmore 1938, USNM 13807

* Type specimen damaged or parts of it missing since original description.

frontal is almost complete, with only the anterior tip missing, but only about half of the right frontal is preserved. The posterolateral corners of both left and right frontals are missing. The roofing osteoscutes are fused to the frontals and the osteoscutal surface is sculptured with tubercular mounds. Grooves on the osteoscutal surface indicate the outlines of the epidermal scutes. The two large frontoparietal scutes are separated by the narrow, wedge-shaped impression of the interparietal. The posterolateral portion of the dorsal surface has a deep incision not covered by osteoscutes. In lateral view the postfrontal depression is small, but the prefrontal impression is extensive and closely approaches the former, indicating that the prefrontal formed the greatest portion of the dorsal border of the orbit. Olfactory processes are well developed, but do not meet ventrally.

The left dentary fragment represents the posterior portion and contains six teeth, the posterior one much smaller than the rest. Spaces for three missing teeth are also present. Some of the crowns are well preserved, exhibiting an anteroposteriorly compressed cutting edge sculptured with vertical striations. The teeth are relatively robust, with an almost uniform diameter along the entire shaft. The intramandibular septum is well developed, and its free ventral border ends under the last tooth. The position of the anterior inferior alveolar foramen is not determinable.

There are two lower jaw fragments, presumably representing the right jaw of the same individual. However, the two fragments do not fit together, and it is assumed that an intermediate piece of this jaw is missing. The larger jaw fragment is composed of the dentary, splenial, coronoid, and surangular. The dentary has six preserved teeth, again the last being much smaller than the rest. The crowns are poorly preserved. The dentary extends posteriad, between coronoid and surangular, to the anterior supra-angular foramen. On the labial surface of the mandible the anterior extremities of the coronoid and the surangular are in the same vertical plane. The splenial is badly damaged. The smaller and more anterior portion of the right dentary has seven partially preserved teeth and space for one. None of the tooth crowns is preserved.

The right maxillary fragment contains two complete teeth and fragments of two others.

The pterygoid fragment is almost entirely covered with small tubercular teeth. The patch at its widest point is about 12 teeth wide.

The body osteoscutes are longer than wide, rectangular, and covered with tuber-

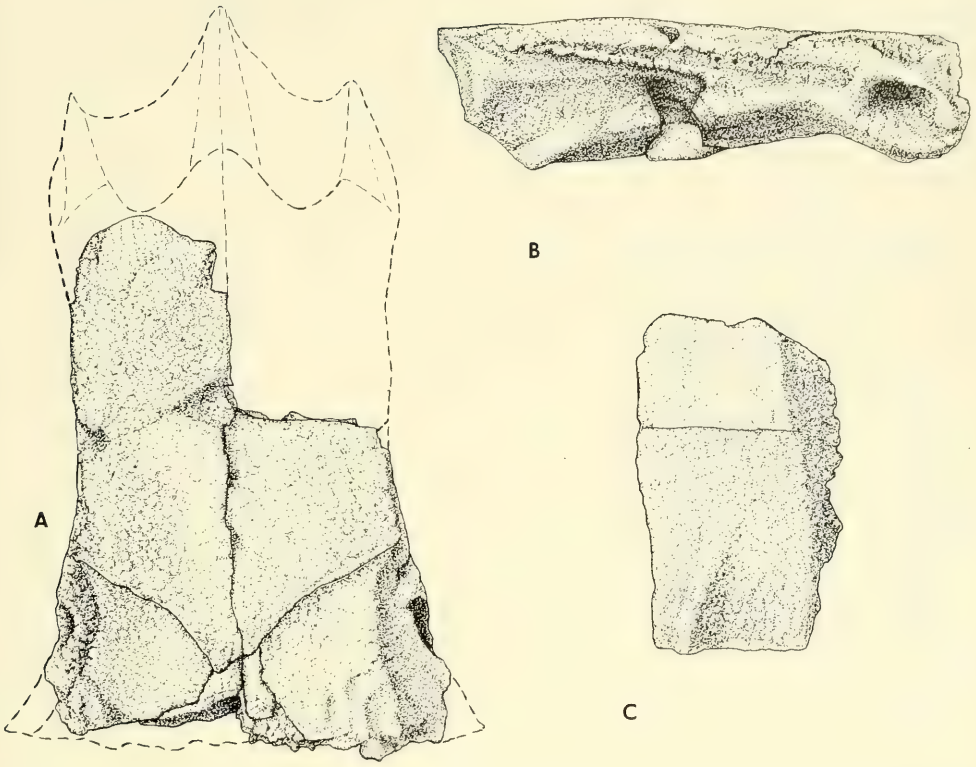

Figure 13. *Xestops vagans*, USNM 16532, holotype frontals and osteoscute. A, left lateral view of frontals; B, the same, dorsal view; C, lateral body osteoscute. All × 4. Frontals restored partially on basis of AMNH 3919. Middle Eocene, Bridger Formation, Wyoming.

cular mounds as in the frontals, but with smooth anterior gliding surfaces indicating the area overlapped by the preceding scute. The gliding surface occupies about one-third of the total length of the entire scute. A lateral overlap is also indicated between adjoining scutes by ventral and dorsal oblique surfaces along the lateral edges. Jagged lateral edges suggest some degree of suturing between osteoscutes. The scutes are keeled, the keels asymmetrical in all but middorsal scutes and extend from an anterior mesial position to the left or right corner, depending on the side of the animal from which they come.

Discussion. The type of *Xestops vagans* consists of isolated fossil elements and the danger always exists that more than one individual may be represented. However, the remains do not include any extra elements that would indicate the presence of more than one individual, and the size of the bones is also consistent with the assumption that they all represent a single individual.

The type frontal was figured by Gilmore (1928, p. 145), and this figure was copied by McDowell (1954, p. 116, fig. 37). Gilmore figured the outline of the frontoparietal scutes, but did not recognize the interparietal epidermal scute impression, giving the figure a pathological appearance. The type, however, clearly shows a triangular interparietal scute impression separating the two frontoparietals at the midline (Fig. 13b).

The frontals of *Xestops vagans,* in having a metopic suture and relatively straight orbital borders, resemble those of the Upper Cretaceous *Pancelosaurus piger* as well as those of Recent diploglossines, ophisaurs, and *Anguis.* The borders of the type frontals appear even straighter as a result of the missing posterolateral corners, which ordinarily expand laterally at the frontoparietal suture. The epidermal scutellation, as indicated on the osteoscutal surfaces, also resembles the above Recent forms, but in *Xestops* and P. *piger* the frontoparietal scutes approach one another somewhat closer at the midline than in Recent anguids. The sculpture of the osteoscutes is, however, very different from that in the above forms, and is identical with that of *Peltosaurus granulosus, Melanosaurus,* and *Glyptosaurus.* In tooth structure *Xestops* also resembles *P. granulosus* and *Melanosaurus* and to a lesser degree *Pancelosaurus piger.* The labial contact of the surangular, coronoid, and angular with the dentary also resembles that found in the above fossils and *Glyptosaurus* with the exception of *P. piger,* but in *P. granulosus* the labial dentary process of the coronoid is slightly in advance of the surangular, whereas in the rest of the above the anterior extremities of these bones are in line, as in *Xestops.* Correlated with this arrangement of bones, the dentary extends posteriad below the coronoid to the anterior supra-angular foramen in these fossil forms.

The body osteoscutes of *Xestops vagans* have beveled lateral edges, indicating that they overlapped laterally as well as anteroposteriorly. This feature and the straight orbital borders of the frontals were utilized by McDowell and Bogert (1954) to refer *Xestops* to the Diploglossinae. The thick, well-ossified, rectangular osteoscutes of *X. vagans* are unlike the thin, subcircular osteoscutes of Recent diploglossines. They bear the closest resemblance, among the Recent forms, to osteoscutes of the ophisaurs, especially those of *Ophisaurus apodus.* The osteoscutes of *X. vagans* also resemble those of *Melanosaurus, Glyptosaurus,* and *Peltosaurus granulosus* in sculpture, in general outline, and in heavy ossification. The osteoscutes of the latter are somewhat thinner than those of *Xestops vagans.* The lateral beveled edges, although very pronounced, are not unique to *Xestops.* The osteoscutes of *Pancelosaurus piger* show pronounced beveled lateral edges, and the osteoscutes of *P. granulosus* also overlapped to a lesser degree. Some indication of lateral overlap is present in a number of other anguid fossils (see also Hoffstetter, 1962, p. 154, fig. 3).

The characteristic pattern of the labial contact of dentary and postdentary bones of the mandible, similar teeth, and a tubercular sculpture of the osteoscutes, relate *Xestops vagans* to the large Eocene and Oligocene fossil forms *Melanosaurus, Arpadosaurus, Glyptosaurus,* and *Peltosaurus.* The epidermal scale imprints on the osteoscutal crust of the frontals of *Xestops* is similar to that found in *Pancelosaurus piger,* and the unfused condition of these bones suggests that *X. vagans* is structurally the most primitive member among the above-listed Eocene and Oligocene fossil genera, and the one most closely related to *Pancelosaurus.*

Hecht (1959, pp. 132–134) described *Dimetopisaurus wyomingensis* from the Middle Eocene Bridger Formation at Tabernacle Butte, Wyoming. The holotype (AMNH 3819) consists of a nearly complete left frontal. On comparison, the type frontals of *Dimetopisaurus wyomingensis* agree in every observable detail with the holotype of *Xestops vagans* (which was unavailable to Hecht at the time of his description). The two frontals agree in total length, osteoscute sculpture, epidermal scale impressions, general shape, and shape of the prefrontal and postfrontal impressions, as well as their distance from one another. The assumption that *D. wyomingensis* is a synonym for *X. vagans* is further strengthened by the fact that Hecht recognized osteoscutes of *Xestops*

from the same sediments from which he described *D. wyomingensis*. Both *X. vagans* and *D. wyomingensis* are known only from Middle Eocene deposits. *D. wyomingensis* is here considered a synonym of *Xestops vagans*.

Only the single species *Xestops vagans* can be recognized with certainty. Four additional Bridger Formation species of *Xestops* were described by Marsh (1872); these are reviewed below. Gilmore (1928) described *Xestops pawneensis* (White River Formation, KU 1281, Gilmore, 1928), which has already been referred above to the new genus *Pancelosaurus*. The holotype of *X. piercei*, USNM 13807, Wasatch Formation (Gilmore, 1938), is a poorly-preserved partial skull, lacking the diagnostic frontals, parietals, and osteoscutes; it is therefore a *nomen nudum*. Gilmore's generic assignment rested on laterally-beveled osteoscutes, and specific distinctness was based on a pitted rather than tubercular osteoscutal sculpture. The osteoscute is heavily worn, and its present sculpture is probably the result of wear. The specimen may be *Xestops vagans* or it may be another anguid.

All of the Marsh holotypes, except that of *X. vagans*, are fragmentary and defy generic assignment, and in one case the type material clearly contains nonanguid remains. The type of *Xestops gracilis* (USNM 16529) consists of four keeled, elongated osteoscutes and may represent those of the tail region of *X. vagans*. The dentary associated with the osteoscutes is not anguid, for the Meckelian groove is closed by bone. The type of *X. lentus* (USNM 16531), consists of two caudal vertebrae with chevrons apparently fused to the centrum. The type species material lacks caudal vertebrae, so that generic reference of caudal vertebrae cannot be regarded as valid, although they would not be an acceptable type in any case. In the original Marsh description of the type of *X. minutus* (USNM 16530), and also noted by Gilmore (1928), a maxilla and a dentary are mentioned. The dentary has either been lost or misplaced. The tiny maxillary fragment contains four teeth that resemble those of *Gerrhonotus* rather than those of *Xestops*, but once again the specimen is too fragmentary for positive generic identification. *X. microdus* (USNM 16528) is represented by a dermal headscute similar to the ones found in *Glyptosaurus*, and a dentary fragment with three complete teeth bearing striated crowns with enameloid covering. The teeth are very slender, with a very strong subdental shelf. The type material also contains a fragmentary vertebra. Here again I can see no reason to assign this fragmentary material to the genus *Xestops*. The cranial osteoscute would indicate a more likely glyptosaurid affinity, though the other material is unidentifiable. *X. gracilis*, *X. lentus*, *X. minutus*, and *X. microdus* are all *nomina nuda*.

Hoffstetter (1962b) has described a very closely related form, *Paraxestops*, from the late Eocene of Switzerland, that will be discussed in a study in progress (Estes and Meszoely, ms.).

Peltosaurus Cope 1872

Type species of genus. Peltosaurus granulosus Cope 1872.

Geological range. Only known with certainty from the Oligocene of North America. Various jaw elements have been referred to this genus, but in view of the great similarities among the teeth of a number of anguid genera of the Eocene and Oligocene, these identifications are very possibly erroneous.

Referred species. Peltosaurus granulosus and *P. abbottii*.

Peltosaurus granulosus Cope 1872

Holotype. AMNH 1610. The type material consists of the following disarticulated skeletal elements: portion of frontals, parietal, premaxilla, greater portions of left and right mandibles, small fragments of left maxilla, jugal, osteoscutes, and verte-

Table III. *Pancelosaurus piger* Skeletal Elements Examined from Various Localities.

	Lance Formation (Late Cretaceous) Wyoming	Hell Creek Formation Bug Creek Anthills (Late Cretaceous) Montana	Bison Basin Locality Tiffanian (Late Paleocene) Wyoming
Dentaries	9	50 +	12
Maxillae	6	50 +	4
Premaxillae	0	1	3
Frontals	3	2	23
Parietals	2	4	4
Pterygoids	0	0	7
Palatines	0	0	4
Osteoscutes	7	40 +	100 +
Vertebrae	5	10	100 +

brae. The type material also includes two blocks of matrix containing osteoscutes and fragments of postcranial elements.

Type locality. Cedar Creek, Logan Co., Colorado.

Horizon. Cedar Creek beds, White River Formation, Middle Oligocene.

Gilmore (1928, pp. 122–135) described the skeleton of *Peltosaurus granulosus* in great detail. Most of his observations are correct, but the emphasis placed by him on certain cranial characters differs from mine, and there are also some corrections and new observations to be added to his description. Not all the skeletal elements of *Peltosaurus granulosus* are redescribed here, but only those that are in my view diagnostic, those that were described erroneously, or those about which my observations differ from those of Gilmore. The description is based on all *Peltosaurus* material available to me (Table IV).

Revised description. The frontals are fused, with gently concave borders. The greater part of the frontals is covered by osteoscutes that are fused to the frontal bones. The osteoscutal crust is covered by raised tubercles. The outline of two large frontoparietal scales is impressed upon the osteoscutal surface, extending anteriad somewhat less than one-half the entire length of that surface. The two frontoparietal impressions make strong medial contact with one another, almost excluding the single medial interparietal scale impression from the frontal bone. The latter is a tiny wedge-shaped impression confined to the medioposterior border of the frontal bone. The posterolateral corners of the frontal are devoid of osteoscutes. The anterior end of the frontal bears two deep, wedge-shaped depressions for the insertion of the nasal bones. Next to these depressions the frontal is also devoid of osteoscutal crust, indicating overlap of this area by the prefrontal osteoscutes. The lateral surface bears two deep incisions: a posterior small one for the postfrontal and an anterior large one for the prefrontal bone. The two incisions are widely separated. The ventral surface is smooth, shows no suturing where the two frontals are fused, and bears the olfactory processes.

The parietal table is wider than long, with a small medial notch in the back. The osteoscutal crust covers more than one-half of the anterior surface of the parietal table, and is covered with the same tubercular mounds as the frontals (Pl. 2). Grooves indicate the impression of paired lateral parietals, a single, medial, wedge-shaped interparietal, and occipital epidermal scales. The latter two are approximately the same size, with the interparietal impression being slightly larger; this impression also bears the parietal foramen. The interparietal impression is relatively much narrower than in the Recent anguids. The temporal wings are expanded.

On the ventral surface (Fig. 16d) a

Plate 2. *Peltosaurus abbottii,* FMNH P12861, holotype skull. Above: dorsal view of skull. Below: Ventral view of same. About × 2. Note wide pterygoid on the figure below. Oligocene, White River Formation, South Dakota.

troughlike depression leads to the parietal fossa, which is located at the apex of a triangular area enclosed by the converging anterior ridges. The parallel raised borders of the trough are formed by the posterior extension of the anterior ridges. The parietal fossa is an anteriorly-directed, slanted pit. Less prominent posterior ridges are present, extending into the temporal processes of the parietal.

No premaxillary foramen is present at the lateral union of maxilla and premaxilla.

The surangular, articular, and prearticular are indistinguishably fused in the mandible. The anterior extremities of the surangular and angular in labial view are set posteriad of the well-developed anterior coronoid process. Labially, the dentary contacts the anterior supra-angular foramen in about half of the specimens, but is excluded in the others. The distance between the anterior extremity of the surangular and the anterior tip of the dentary is nearly the same as from the former point to the posterior limit of the dentary. The latter distance is slightly greater. A small dorsal process of the dentary extends posteriad over the leading edge of the coronoid. On the lingual surface both dentary and splenial are involved in the formation of the anterior inferior alveolar foramen, which is under the fifth and sixth teeth from the rear (Fig. 17a).

The disarticulated dentary (Fig. 10d) exhibits a Meckelian fossa that is ventral anteriorly and extends to the tip of the dentary. The intramandibular septum is fused ventrally with the rest of the dentary. The septum is notched and the anterior extremity of the notch is under the fifth tooth, almost in line with the anterior inferior alveolar foramen. The dentary bears about 21 teeth. The most posterior tooth is the smallest, and the teeth increase in size to about the fifth tooth from the rear; after that they are subequal in size. The apices of the crowns of the teeth bear a cutting edge that is set almost parallel to the long axis of the mandible but directed at an anteroposterior angle. The crowns bear striations set at a right angle to the cutting edge, and lack a dark enameloid covering. Some of the crowns are slightly expanded in a fan-shaped fashion in an anteroposterior direction.

The occipital condyle was described by Gilmore (1928) as follows: "The occipital condyle is reniform and relatively small as in *Gerrhonotus* and *Ophisaurus*. It is presumed that the exoccipitals contribute to the formation of the condyle but the coalescence of the sutures does not permit of a determination of this fact." The fused condition as described by Gilmore exists in most of the specimens examined, but in a small specimen of *Peltosaurus granulosus* (FAM 42915) the occipital condyle is clearly tripartite. In this specimen the three bones contribute nearly equally to the condyle formation, with the basioccipital contributing a little more than either the left or right exoccipital.

The osteoscutes are unkeeled, rectangular, and are covered with raised tubercular mounds; the smooth gliding surface makes up about one-third the total length. The osteoscutes have well-defined oblique surfaces along their lateral edges, one dorsal and the other ventral, indicating prominent overlap between adjacent osteoscutes. A lateral fold was probably present (KU 1280).

In the literature dealing with *Peltosaurus granulosus* the concept that it is very closely related to the Recent *Gerrhonotus* is firmly entrenched. This may be the result of three factors: (1) the historical treatment of *Peltosaurus granulosus;* (2) little or no knowledge of the cranial anatomy of pre-Eocene anguid fossils; (3) the fused frontals found in *Peltosaurus*, which among the Recent forms, occur only in the gerrhonotines *Gerrhonotus* and *Abronia;* (4) gerrhonotines share a similar type of body scutellation with *Peltosaurus*.

Cope, who described *Peltosaurus granulosus*, referred this fossil to his family

Gerrhonotidae. Later, Gilmore (1928) described *Peltosaurus* in great detail and made frequent comparisons with *Gerrhonotus*, probably in part the result of his limited comparative material. He apparently had only two *Gerrhonotus multicarinatus* and three *Ophisaurus ventralis* skeletons, and so far as is known, no *Diploglossus* material. It also should be pointed out that his comparisons did not always show close resemblance between the skeletons of *Peltosaurus* and *Gerrhonotus*. Tihen (1949) also included *Peltosaurus* along with *Melanosaurus* in the limbed Gerrhonotinae. McDowell and Bogert (1954, p. 115), suggesting a close relationship between *Peltosaurus* and *Gerrhonotus liocephalus*, gave a list of characters common for these two forms: (1) large frontonasal in contact with frontal scute; (2) two frontoparietal scales in medial contact separating the frontal and interparietal scales; (3) maxilla and frontal bones in contact; (4) left and right frontals indistinguishably fused. These points will be considered below.

(1) A frontonasal and frontal scute contact is not unique to these two anguids, but also occurs in *Ophisaurus apodus* and *Diploglossus monotropis*. (2) It is true that in both *Peltosaurus* and *G. liocephalus* the frontoparietal scales are in contact, but in *G. liocephalus* this contact is narrow, with the scales just touching along their anterior border, whereas in *Peltosaurus* the two scales are in contact almost along their entire length. (3) Maxillofrontal contact is again not unique to the two forms, but occurs in the Recent *Diploglossus* as well as in *Glyptosaurus*. (4) Fused frontals are found in *Gerrhonotus*, but occur also in *Melanosaurus* and some *Glyptosaurus*. It also may be pointed out that in *Peltosaurus* the postorbital and the postfrontal bones are fused, whereas they are always separate in *Gerrhonotus*, but fusion also occurs in some recent diploglossines.

The detailed study of *Pancelosaurus piger* presented above indicates the following conclusions in regard to *Peltosaurus*. (1) The tubercular sculpture in *Peltosaurus* is not primitive, but aberrant, and is found only in Eocene and Oligocene forms and in the Recent *Gerrhonotus imbricatus*. (2) The strong medial contact of frontoparietal scales in *Peltosaurus* is not derivable from the relatively widely-separated frontoparietal scales of *Pancelosaurus piger*, without passing through a stage such as is found in modern *Gerrhonotus*, where these scales are barely touching. Thus this condition also appears to be aberrant. (3) The scalation of the parietal, as indicated by impressions, is again unlike Recent forms or *P. piger*. The interparietal and occipital scales are nearly equal in size in *Peltosaurus*, whereas in *Pancelosaurus piger* and the Recent forms the interparietal is much larger than the tiny occipital.

Thus, while perhaps *Peltosaurus* bears the most superficial resemblance among the large Eocene and Oligocene fossils to the Recent forms, its affinities are with the former group (*Peltosaurus, Xestops, Melanosaurus, Arpadosaurus, Glyptosaurus*), all members of which bear a granular tubercular sculpture on their osteoscutes absent in *Pancelosaurus piger*, which shares its pit-and-groove sculpture with the Recent forms. Also, the above large fossil anguids have a mandible in which the intramandibular septum is fused, and the anterior extremities of the coronoid and surangular bones are in a vertical plane on the labial surface (*cf.* Figs. 3, 17). In *Peltosaurus* (Fig. 17a) the coronoid extension is anterior to the surangular in contrast to Recent forms in which the latter bone always extends far anterior to the former. These conditions are not the result of size, since my comparative material includes some very small *Peltosaurus* skulls, the smallest measuring 29.9 mm, while the largest Recent skull, *Diploglossus occiduus*, measures 44.5 mm.

A number of pre-Oligocene fossil forms earlier referred to the genus *Peltosaurus* were referred above to the genus *Pancelosaurus*. The generic identification of *Pelto-*

TABLE IV. *PELTOSAURUS* SPECIMENS EXAMINED FOR THIS STUDY.

AM	1610—skull and mandible fragments (type of *P. granulosus*)
	1652—skull and jaws, nuchal scutellation
	8138—skull and jaws, nuchal scutellation
FAM	42913—skull and jaws
	42915—skull and jaws
	42917—isolated frontals and parietals
	——— —isolated parietal
FMNH	UR450—fragmentary skull and jaws of two individuals
	UR452—fragmentary right ramus
	UR453—left mandible
	UC391—skull, jaws, anterior body region, shoulder girdle
	UC1720—partial skull and jaws
	P12861—skull (type of *P. abbottii*)
	P25806—partial right mandible
	P27072—skull and jaws
KU	620—frontals, parietals, and isolated fragments
	1278—frontals and mandibular fragments
	1282—left dentary
	1283—mandible fragments
	1284—mandible fragments
	7654—many isolated fragments
	7661—skull, jaws, and fragments
	12957—frontals
	12958—mandible fragments
	12959—left maxilla
	12961—frontals
	12962—right dentary
U. Minn.	VP-1511—skull, jaws, nuchal scutellation
USNM	1280—skull and jaws
	13870—skull and jaws
	15607—frontals
YPM	621—dentaries
	1061—skull and jaws

saurus from other than Oligocene deposits almost invariably has rested on tooth structure, even though Gilmore's observations should have been a warning against such actions. He wrote (1928, p. 146) describing the teeth of *Xestops vagans*: "As a whole they are practically indistinguishable from the teeth of *Peltosaurus*"; again (p. 142), in his description of *Melanosaurus*: "The dental formula of *Melanosaurus maximus* appears to be very similar to that of *Peltosaurus*"; and, again, in the description of *Pancelosaurus* ("*Peltosaurus*") *piger* (p. 136): "The structure of the teeth, as mentioned above, is remarkably like that of *Peltosaurus*, but similar teeth are found in the very large *Glyptosaurus hillsi*." As clearly indicated from these quotes and confirmed by my observations, similar teeth are found in at least four fossil genera; tooth structure is therefore a very poor criterion for generic identification in fossil anguids.

Diagnostic cranial elements of *Peltosaurus*, such as frontals and parietals, are presently known only from Oligocene deposits, and there is therefore no good reason to recognize this genus from any deposits of any other age, although better material may in the future confirm time extensions in either direction.

Peltosaurus abbottii Gilmore 1928

Holotype. FMNH 12861, nearly complete skull.

Type locality. Cottonwood Creek, Washington Co., So. Dakota.

Horizon. Leptauchenia Zone (*Protoceras* beds), White River Formation, Upper Oligocene.

Gilmore (1928, p. 135) described this species as follows: "The great breadth of the skull back of the orbits, the more regular convex profile of the upper anterior half, and the presence of a large subtriangular frontonasal scute bordered on either side by a single large prefrontal scute appear to indicate its specific distinctness from *Peltosaurus granulosus*."

Discussion. Peltosaurus abbottii is known only from a single specimen (Pl. 2). It is damaged in the cheek region on both sides, where the postfrontal articulates with the jugal, but these two bones are still in contact on the right side. Frontal and parietal bones are also slightly disassociated from one another at the frontoparietal suture, and the extremities of both of these bones are pressed downward by the sediment. These facts caution against placing much emphasis on the shape or breadth of the

skull, but certain other features exhibited by the specimen are perhaps indicative of a specific distinctness of this fossil from *Peltosaurus granulosus*. The frontonasal scute is broader, less elongate, and more triangular in *P. abbottii* than in *P. granulosus*. The interparietal scute incision, instead of being single, medial, and wedge-shaped, is paired and set to the side. The part of the pterygoid bone bearing the teeth is also relatively broader and more robust than in *P. granulosus*. Both pterygoids, as well as palatines, bear teeth as in *P. granulosus*. In all of its other known characters *P. abbottii* agrees with *P. granulosus*.

Although the differences discussed above appear to be minor, it should be pointed out that many diagnostic specific features used by modern herpetologists would probably not be preserved in the fossil forms. The species *P. abbottii* is recognized here with some hesitancy.

Melanosaurus Gilmore 1928

Xestops Camp (1923, p. 328).

Type species of the genus. Melanosaurus maximus.

Geological range. Known only from North American deposits of early Eocene age.

Referred species. The genus is represented by a single species, *Melanosaurus maximus.*

Melanosaurus maximus Gilmore 1928

Holotype. AMNH 5168. The type material consists of a block of matrix containing most of the compressed skull elements of one individual, and two smaller blocks containing vertebrae and osteoscutes. Isolated elements referred to this specimen include: greater portion of the right mandible, two maxillary fragments, a vertebra, and several osteoscutes.

Horizon. Wasatch Formation, "Above red-banded beds," Lower Eocene.

Type locality. Clark's Fork Basin, Big Horn County, Wyoming.

Revised description of the holotype. On the block containing the skull elements, the following bones are visible on the dorsal surface: frontal, parietal, jugal, supratemporal, quadrate, prefrontal, postorbital, postfrontal, coronoid, fused surangular-articular-prearticular, squamosal, and a small portion of the dentary.

Ventrally the following bones are visible: right dentary, vomers, palatines, pterygoids, basisphenoid, basi- and exoccipitals, left epipterygoid, right quadrate, and postfrontal.

Frontals: The frontals are fused; their lateral borders are gently concave in the orbital region. The maximum length of this bone is 29.2 mm and the maximum width along the frontoparietal suture is 22.8 mm. The roofing osteoscutes are coossified with the underlying bone, and are covered with tubercular mounds. Both lateroposterior corners are devoid of osteoscutal crust. Faint grooves are present on the surface and possibly indicate the outlines of two large frontoparietal and two smaller scales. The latter appear to be halfmoon-shaped and adhere to the anterior border of the frontoparietal. None of these is clearly defined, and thus they do not allow for positive statement regarding the epidermal scalation in this region.

Parietal: The parietal is covered with the same tubercular mounds as the frontals. Here faint grooves on the osteoscutal surface indicate the outline of interparietal and occipital epidermal scales. Both are relatively narrow and nearly equal in size. The former is triangular and bears the parietal foramen close to its posterior extremity. Two large, loosely-attached osteoscutes are present lateral to the occipital scale impression. The parietal table along the midline is 23.1 mm long. The proximal portion of the left supratemporal process bears a deep groove along its mesial border.

Jugal: The left jugal is roughly rectangular and is missing a large portion at the junction of the maxillary and the temporal processes. The posterior border of the temporal process is covered with minute ridges.

Squamosal: The squamosal is long, with a chord length of 30.0 mm.

Postorbital: The left postorbital now lacks the anterior portion, which was illustrated by Gilmore (1928, fig. 86) as covering the postfrontal.

Postfrontal: The left postfrontal is a tripartite bone with frontal, parietal, and well-developed jugal processes. The right postorbital located on the ventral surface bears a deep postorbital incision on its posterior border.

Quadrate: The quadrate has an extremely well-developed internal wing, which is exposed on the ventral surface of the block containing the skull elements.

Pterygoid: The pterygoids, palatines and vomers all bear teeth. In the first two the tooth patches are very large. The vomerine teeth form a narrow patch. Some of these minute teeth have sharp points and are recurved.

Occipital: The occipital region is badly damaged; very little of the natural surface is preserved.

Mandible: The anterior extremities of both dentaries are missing. The breakage on both occurred at nearly the same point, as shown by a tooth count of 11 in both dentaries. The right dentary contains seven complete teeth, the left dentary has only four; the rest of the teeth are fragmentary. The teeth are robust, with bluntly chisel-shaped crowns, which are compressed into slightly arched cutting edges, the main axis of which are parallel to the long axis of the jaw. Striations are present mostly at a right angle to the cutting edge. On the right mandible the contact of the dentary with the coronoid, surangular, and angular is visible, and the anterior extremities of the latter bones on the labial surface are in the same vertical plane. The anterior inferior alveolar foramen is between the dentary and the splenial. The dentary extends between the coronoid and the surangular to the anterior supra-angular foramen. The articular, surangular, and the prearticular are fused. The articular facet (preserved on the left mandible) is roughly elliptical, with the chorda tympani foramen posterior to the facet and the anterior articular foramen in front of the facet.

Maxilla: A medial portion of both maxillae is preserved. Both fragments contain spaces for seven teeth, but in both maxillae only five are complete. The teeth are essentially the same as described for the dentary. The anterior labial surface of both fragments is covered by osteoscutes.

Osteoscutes: The body osteoscutes have the same tubercular mounds as on the osteoscutes fused with the skull elements, and only about one-fourth the total length of the scute is occupied by the smooth gliding surface. The gliding surface and the sculptured surface are separated by a deep groove. The lateral edges of the osteoscutes have very well-developed suture surfaces. Only one osteoscute among the many in the type material is keeled.

Paratype. AMNH 5175. Isolated cranial and postcranial elements of a slightly larger individual than the holotype. The paratype material consists of the following disarticulated skeletal elements: frontals, parietal, premaxilla, right and left maxillae, right jugal, both quadrates, right dentary fragment, fused articular and surangular of the right mandible, other smaller mandibular fragments, vertebrae, and osteoscutes.

Locality. Big Horn Basin, Big Horn Co., Wyoming.

Horizon. Wasatch Formation, Lower Eocene.

Partial redescription. The paratype consists of isolated skeletal elements, and consequently the ventral surfaces of such diagnostic bones as the parietal and frontals are visible. The paratype material contains

a premaxilla and numerous body osteoscutes, presumably from the posterior part of the body. Only those elements important to the discussion will be described below. For a more complete description the reader is referred to Gilmore (1928, pp. 138–144).

Frontals: The frontals are roughly triangular, with a maximum width of 30.2 mm and a maximum length of 34.5 mm. The corners of the frontals are rounded by wear, and the osteoscutal crust on the dorsal surface is badly eroded. A few pustules are present similar to the ones on the holotype. No impressions of epidermal scales are visible. Olfactory processes are present on the ventral surface and do not meet on the midline. Lateral prefrontal and postfrontal incisions are present and separated from one another by a narrow gap of 4.8 mm.

Parietal: Most of the parietal table of the paratype is preserved, but both of the supratemporal processes of this bone are missing. The parietal table is relatively elongate with gently concave lateral borders. It has a maximum width of 28.0 mm along the frontoparietal suture and a maximum length of 24.5 mm. The osteoscutal crust is badly eroded here as well, and no epidermal scale impressions are visible on the dorsal surface. On the ventral surface (Fig. 16a) the well-developed anterior ridges converge posteriorly, forming a triangular area that encloses the parietal foramen and extends posteriad to the parietal fossa. The parietal fossa is an anteriorly-directed, slanted pit. The posterior ridges emerging from the supratemporal processes converge on the anterior ridges at the level of the parietal fossa.

Premaxilla: The rostral body is relatively short and robust and bears a pair of prominent labial foramina. In anterior view the lateral margins of the rostral body are straight and converge from both sides on the nasal spine. There is no marked constriction between the nasal spine and the rostral body. The rostral body has a chord length of 14.6 mm as measured between the lateral extremities of the maxillary processes; there is a distance of 5.8 mm from its ventral margin to the point at which it gives off the nasal spine. The preserved portion indicates a tooth count of eight. Much of the morphology of this bone is concealed by hematite fused to the lingual surface.

Osteoscutes: The osteoscutes of the paratype display sculpture in which the tubercular mounds are arranged in concentric rectangles. The smooth gliding surface occupies a little over one-fourth the total length of the entire scute and is separated from the sculptured surface by a deep groove. The gliding surface is in the shape of a rectangular transverse band. The lateral surface of the scutes is highly irregular, indicating a high degree of lateral suturing between osteoscutes. A number of the osteoscutes bear keels, and all have numerous small foramina on their under surfaces.

Discussion. Camp (1923) based his *Xestops* restoration on AMNH 5168. Gilmore (1928) referred this specimen to a new genus and species, *Melanosaurus maximus*. He noted that it resembled *Peltosaurus granulosus* in having fused frontals with concave borders, and referred *M. maximus* to the family Anguidae. McDowell and Bogert (1954), while remarking that *Melanosaurus* in general shows, "a very specialized diploglossan morphology with much resemblance to such primitive Anguidae as *Gerrhonotus* or *Diploglossus*," referred *M. maximus* to the family Xenosauridae on the basis of the following six points:

1. The presence of an epiphysis of the paroccipital process as a separate ossicle.
2. The presence of an inner, wing-like conch on the quadrate.
3. Much dilated and sculptured postorbital ramus of the jugal.
4. Coossification of the cranial osteoderms with one another, as well as with the underlying bones.

Table V. Distribution of Some Character-states in Recent and Fossil Anguids.

	Pancelosaurus piger	*Peltosaurus granulosus*	*Melanosaurus*	*Ophisaurus*	*Diploglossus*	*Gerrhonotus*	*Glyptosaurus*
Frontals distinct	+	−	−	+	+	−	+(−)
Skull elements ornamented with tubercular mounds	−	+	+	−	−	−	+
Osteoscutes with prominent lateral overlap	+	+	−	+	+	+	−
Osteoscutes rectangular with transverse band-shaped gliding surface	+	+	+	+	−	+	+
Toothed pterygoids	+	+	+	+	−	+	+
Toothed palatines	+	+	+	+	−	−	+
Toothed vomers	?	−	+	+(−)	−	−	−
Frontoparietal scales separated by interparietals	+	−	?	+	+	+(−)	−

5. Lack of anterior expansion of the frontal, anterior to the orbital emargination.
6. Indications of a longitudinal crest along the temporal arch.

Each of these points will be considered below:

1. The exoccipital and prootic region of the holotype is damaged; the smooth surface bone layer is nowhere preserved in this region. It is only by comparison and by knowing the region where the prootic occurs that one can recognize this bone. The element referred to by Camp as the paroccipital appears as a separate piece, but may very well be a flake from the prootic region. Similar conclusions were reached by Hecht (1959). This small element bears little resemblance to the so-called "epiphysis" of the paroccipital of *Xenosaurus*. Estes (personal communication) has observed similar ossicles to those of *Xenosaurus* in some recent anguids (e.g. *Gerrhonotus multicarinatus*, MCZ 32250).

2. The holotype of *Melanosaurus maximus* shows a very large inner wing on the quadrate, as indicated by McDowell and Bogart, but the three *Xenosaurus grandis* skeletons in my possession show practically no development of this inner wing. However, the anguid *Ophisaurus apodus* has a well-developed internal wing of the quadrate, although it is smaller than that of *Melanosaurus*.

3. On the jugal of *Melanosaurus maximus* the postorbital and maxillary processes meet at a right angle, while the postorbital process of *Xenosaurus grandis* is strongly tilted caudad. The striations of the jugal are confined to the posterior and ventral border; similar striations also occur in some glyptosaurs, to which the jugals of *Melanosaurus* bear the closest resemblance. There is little resemblance between the jugal of *Melanosaurus* and that of *Xenosaurus*.

4. The coossification of cranial osteoderms with the underlying bones is an anguid character as well as a xenosaurid one. However, frontals of *Xenosaurus grandis* are covered with large raised osteoscutes that are coossified, and lines indicating the position of the epidermal scales

are absent. The skull roofing bones of *Melanosaurus* are covered by osteoscutes bearing a sculpture similar to that of *Xestops* or *Peltosaurus granulosus*, and the parietal osteoscutes clearly show the outline of interparietal and occipital epidermal scales characteristic for nearly all anguids, excepting *Glyptosaurus*.

5. The outline of the frontals (especially that of the paratype) bears an extremely close resemblance to that of some glyptosaurs (e.g. *G. rugosus*) and shows little resemblance to the emarginated, narrow frontals of *Xenosaurus grandis*. The frontal outline of the latter bears the closest superficial resemblance among Recent anguids to that of *Gerrhonotus liocephalus*.

6. It is difficult to comment on this statement, since it may refer to the supratemporal processes of the parietal or to the squamosal. It probably refers to the latter bone. The squamosal in *Melanosaurus* is very long and slender, whereas in *Xenosaurus* it is short and thick, with a posteriomesial weblike process that is in contact with the parietal, roofing over most of the upper temporal opening. The supratemporal processes of the parietal are also elongate, whereas in *Xenosaurus* these two are very short and stubby.

Gilmore (1928, p. 138) suggested that *Melanosaurus maximus* "has its nearest affinities with the genus *Peltosaurus*." There is a resemblance between *Peltosaurus granulosus* and *Melanosaurus* in that they both have fused frontals with concave orbital borders. The outline of the frontals of the holotype also resembles that of *P. granulosus*, while that of the larger paratype is closer to *Arpadosaurus* (see below) and *Glyptosaurus*. Sculpture type of the cranial osteoderms is essentially the same as in *P. granulosus*, but the same sculpture type also occurs in *Xestops*, *Arpadosaurus*, and *Glyptosaurus*. There is a similarity between the pattern of labial articulation between dentary and postdentary bones of *Melanosaurus* and *P. granulosus;* but the similarity is even greater between *Melanosaurus* and *Glyptosaurus*. The heavy, sutured osteoscutes have a deep groove between the gliding surface and the sculptured surface and are very similar to those of *Glyptosaurus;* they resemble less the thin, essentially beveled scutes of *Peltosaurus granulosus*, which also lack the groove between gliding and sculptured surfaces. Also, with respect to size, *Melanosaurus* (especially the paratype) is in the range of the genus *Glyptosaurus*. *Melanosaurus* is more primitive than *P. granulosus* in having toothed vomerine bones and in having separate postorbital and postfrontal bones.

Thus, *Melanosaurus* shares a number of characters with *Peltosaurus granulosus*, but the majority are not unique to the two genera, being found also in other Eocene and Oligocene forms and thus may be regarded as specialized features characterizing a side line of anguid evolution. However, *M. maximus*, with regard to body scutes as well as size, shows a specialization toward the *Glyptosaurus* line. This specialization is not present in *P. granulosus*, whose geological occurrence is later (Oligocene) than that of the Eocene *M. maximus*. The affinities of *Melanosaurus* and *Glyptosaurus* are further discussed in the section dealing with *Arpadosaurus*.

Camp (1923) figured the reconstructed skull of *Melanosaurus* ("*Xestops*") *maximus* based on the holotype, and Gilmore (1928, p. 140) refigured Camp's reconstruction. In this figure, the postorbital is shown to exceed the postfrontal anteriorly, but examination of the holotype indicates a postorbital incision on the posterior border of the postfrontal bone, suggesting that the postorbital was excluded from the orbit, as in the glyptosaurs. It may be also pointed out that Gilmore's photographs of the vertebrae (pl. 23) and the jugal (pl. 24) do not represent the holotype (as indicated in the plate legend), but are skeletal elements of the paratype AMNH 5175.

Arpadosaurus gazinorum n. gen., n. sp.

Holotype. USNM 25826. The type material consists of disarticulated skull elements, osteoscutes, and fragments of vertebrae. The following skull elements have been identified: frontals, parietal, left and right dentary fragments, tip of the right maxilla, fragments of left and right palatines, right articular, and occipital condyle.

Horizon. Late early Eocene.

Locality. Twelve miles north of Big Piney, Wyoming; Wasatch Formation.

Diagnosis. A large anguid structurally intermediate between *Melanosaurus* and *Glyptosaurus* in scalation. *Arpadosaurus gazinorum* differs from the former in having an unusual epidermal scalation, as indicated by grooves on the frontal bone, and a less extensive patch of palatine teeth; from the latter it differs in that the head osteoscutes are not broken up into polygonal plates.

Etymology. Árpád—name of a 10th Century Hungarian leader who was lifted on shields into the air by his peers when they elected him as head of the seven tribes then inhabiting Hungary. The name refers to the shield-shaped fused frontal bones of the lizard. Greek, *sauros*—lizard. The specific name honors C. L. and Chester Gazin, who collected the specimen.

Description of skeletal elements. The frontals (Fig. 14) bear a dorsal metopic suture on the osteoscutal crust but are indistinguishably fused ventrally. They are roughly triangular in outline and short in relation to their width. Their maximum length is 32.8 mm, and they are 28.6 mm along the frontoparietal suture. The dorsal surface of the bone is covered by fused osteoscutes, which have a sculpture of small tubercular mounds. The frontal osteoscutal crust is traversed by numerous grooves, indicating the outlines of epidermal scales. A prominent groove traverses the frontal transversely about one-third the distance of total length of this bone from the frontoparietal suture. Posterior to the above

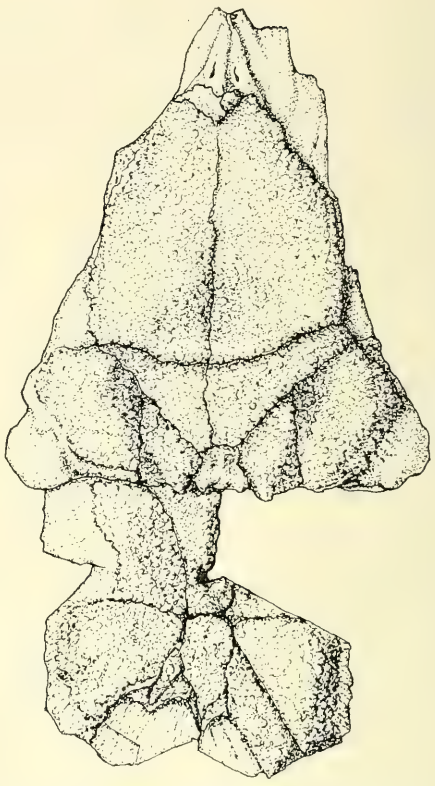

Figure 14. *Arpadosaurus gazinorum*, n. gen., n. sp., USNM 25826, holotype. Frontals and parietals, dorsal view, × 2. Early Eocene, Wyoming.

groove the dorsal surface of the frontal is further subdivided by several grooves. Two grooves, corresponding to the outline of frontoparietal scutes in other anguids, converge on one another toward the posterior midline, but are separated from one another by a small wedgelike area devoid of osteoscutes, presumably representing the interparietal epidermal scute area. The frontoparietal areas are again subdivided into unequal halves by a groove parallel to the metopic suture. On the lateral surface the prefrontal and postfrontal incisions are well defined. The prefrontal incision is the larger, occupying about two-thirds of the lateral surface of the frontal and separated from the postfrontal by only a 3 mm gap. The anterior extremities of the

Table VI. New World Fossil Record of the Anguidae.

	Gerrhonotinae	Anguinae	Glyptosaurinae	Diploglossinae
Pleistocene		*Ophisaurus ventralis* *O. compressus*		*Diploglossus* spp. from Jamaica and the Dominican Republic (Etheridge, 1964, 1965)
Pliocene	*Paragerrhonotus* *Gerrhonotus*	*Ophisaurus attenuatus*	Osteoscutes noted by Estes and Tihen, 1964	
Miocene				
Oligocene		*Pancelosaurus pawneensis*	*Peltosaurus abbottii* *P. granulosus* *Glyptosaurus* (3 species)	
Eocene	*cf. Gerrhonotus*		*Glyptosaurus* (8 species) *Arpadosaurus gazinorum* *Melanosaurus maximus* *Xestops vagans*	
Paleocene		*Pancelosaurus piger*		
Late Cretaceous	*cf. Gerrhonotus*	*Pancelosaurus piger*		

olfactory processes are broken off. Posterior to these processes wedge-shaped impressions are present close to the posterior lateral extremity of the frontal.

The parietal (Figs. 14, 16c) is a quadrangular bone; most of its upper right quadrant is missing. The supratemporal processes are not preserved. Most of the dorsal surface of the parietal, except a small posterior area, is covered by coossified osteoscutes, which are covered with the same tubercular mounds as the frontals. Grooves indicating the outline of interparietal and occipital scutes are present. The interparietal area is narrow and triangular, its apex directed posteriad and enclosing the parietal foramen. The occipital scale impression is subequal to the interparietal, but is subrectangular rather than triangular in shape. Large paired parietal scutes flank the interparietal area, and two similar ones flank the occipital. The occipital area mesial to the two large parietal scutes is also flanked by numerous elongate wedge-shaped irregular scutes.

On the ventral surface two anterior ridges converge posteriad to merge and continue as a single median ridge. The

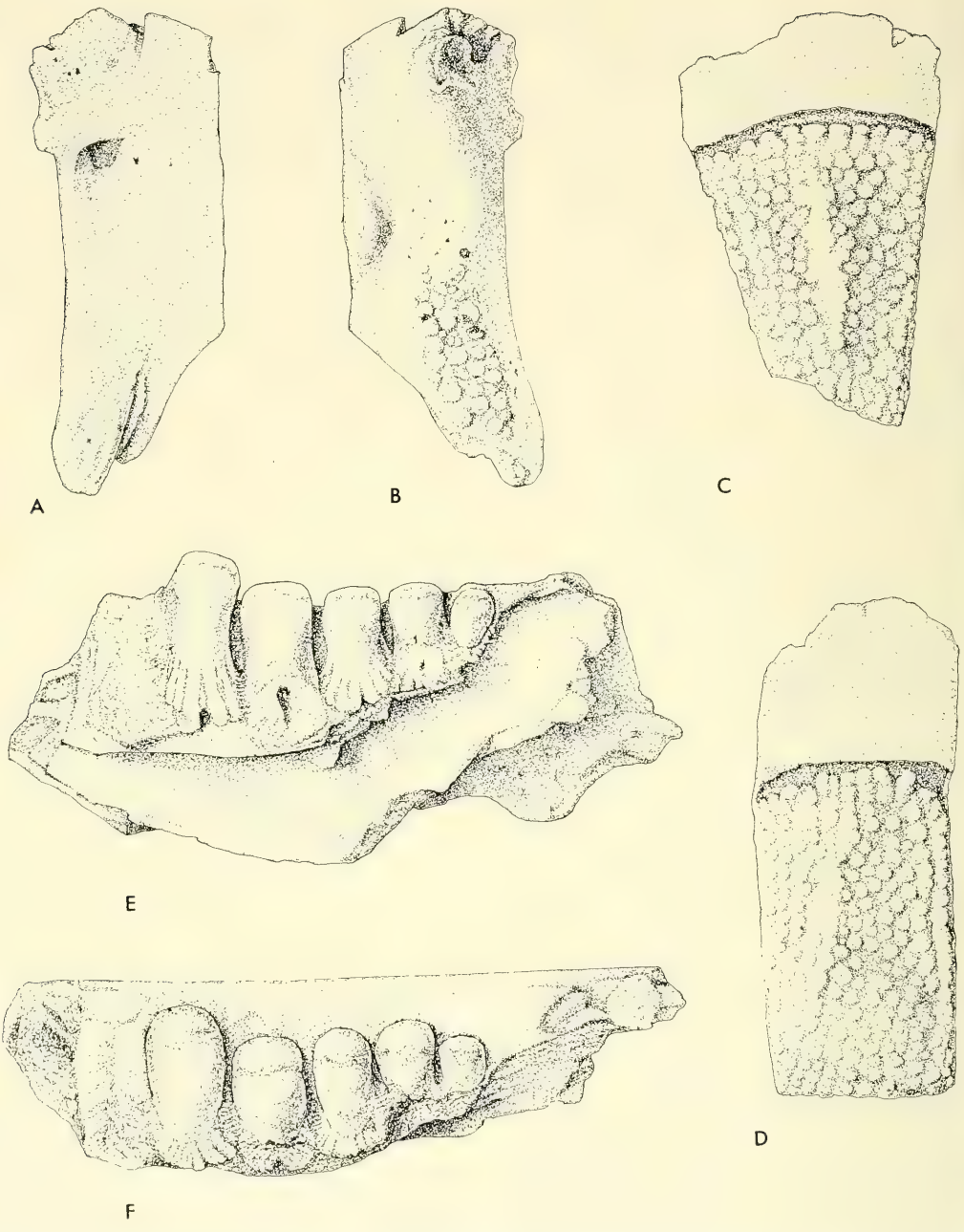

Figure 15. *Arpadosaurus gazinorum*, n. gen., n. sp., USNM 25826, holotype. A, left palatine, dorsal view; B, the same, ventral view; C, medial body osteoscute; D, lateral body osteoscute; E, right dentary fragment, lingual view; F, the same, dorsal view. All × 4. Early Eocene, Wyoming.

area surrounded by the anterior ridges is triangular and contains the parietal fossa close to its posterior apex. The parietal fossa is a vertical pit. The posterior ridges are less prominent than the anterior ones, and merge with the latter at a distance about one-half the total length of the parietal.

The posterior portions of both dentaries are preserved. The right fragment (Fig. 15e-f) contains five teeth, the left only four. The teeth increase in size anteriorly; the most anterior tooth is the largest on both fragments. The teeth are robust crushing teeth with blunt, rounded crowns. In dorsal view the crowns are transversely widened, and have weak, longitudinal cutting edges, from which fine ridges extend at a right angle. The bases of the teeth are expanded and weakly striated. The first, second, and fourth teeth of the right dentary fragment have a basal foramen, and the bases of the latter two are excavated. In the right fragment, the anterior labial coronoid articulation surface ends under the first tooth from the rear; both fragments indicate that on the lingual side the coronoid reached the fourth tooth from the rear.

A small portion of the lower jaw in the articular region includes the jaw articulation surface, which is roughly saddle-shaped and raised anteriorly and posteriorly. Close to the articular facet two foramina occur, one posteromesial and the other anterolateral. The former corresponds to the foramen for the chorda tympani, the latter is the anterior articular foramen.

The greater portion of the right palatine is preserved, with a well-defined patch of tubercular teeth on its ventral surface (Fig. 15a-b). The teeth approach closely, but do not extend as far as, the choana. On the dorsal surface, posterior to the maxillary process, a large, well-defined infraorbital foramen is present. The vomerine process is broken near its base.

The occipital condyle of the occipital region is robust and semi-circular, kidney-shaped in outline. The basi- and exoccipital contributions to the condyle are indistinguishable, as a result of coossification of these bones.

The body osteoscutes (Fig. 15c-d) are longer than wide and covered with the same tubercular mounds as those fused to the frontal and parietal bones. The sculptured surface is separated from the smooth anterior gliding surface by a deep groove. The gliding surface occupies one-third to one-fourth the entire length of the osteoscute. Most of the osteoscutes are rectangular, some with an asymmetrical keel. Other osteoscutes are wedge-shaped, the apex directed posteriad; all of these bear keels. The lateral edges are beveled, and at the same time the irregular surfaces present in this region indicate suturing between adjacent osteoscutes.

Discussion. *Arpadosaurus gazinorum* is known only by a single specimen from what Gazin (1962) refers to as the La Barge fauna. It is comparable in size to the paratype of *Melanosaurus maximus* and to *Glyptosaurus rugosus.* In the general shape of the frontals, and in having rectangular body osteoscutes that are sutured to one another laterally, *A. gazinorum* also resembles the above genera. However, in a number of characters *A. gazinorum* is intermediate between *Melanosaurus maximus* and *Glyptosaurus rugosus.*

On the ventral surface of the parietal (Fig. 16) the triangular area enclosed by the anterior ridges is largest in *Melanosaurus,* smallest in *G. rugosus,* and intermediate in *A. gazinorum.* These same ridges converge in *G. rugosus* to form a narrow but high mesial ridge. This same mesial ridge is broad and flat in *Melanosaurus;* the anterior ridges continue side by side instead of forming a strong single ridge, as in *G. rugosus.* The situation in *A. gazinorum* is once again intermediate. *Arpadosaurus* resembles *Glyptosaurus* in that the parietal fossa is a vertical pit. *Melanosaurus* has a slanted parietal fossa. The general proportions of the parietal table of the

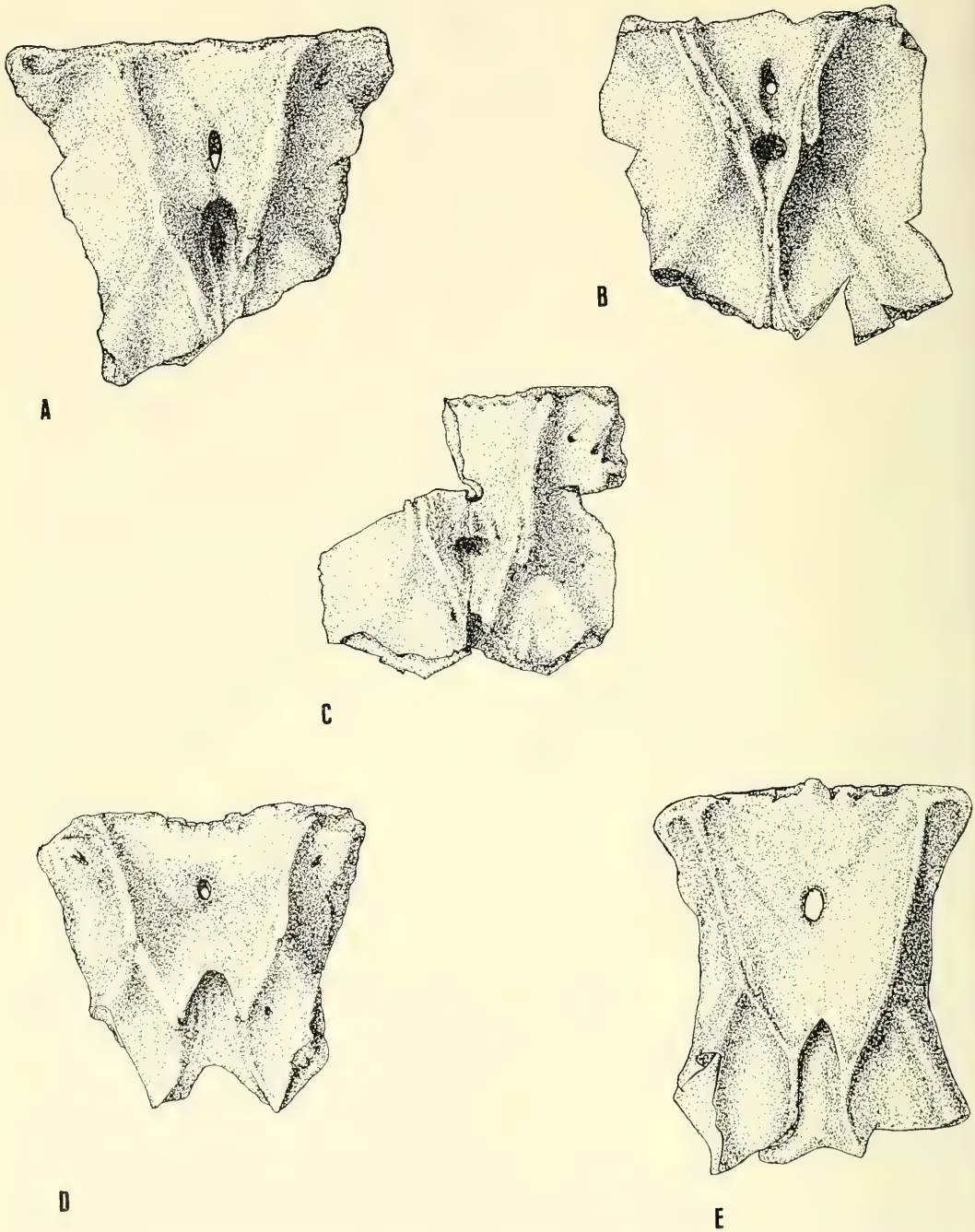

Figure 16. Parietals of fossil anguids in ventral view. A, *Melanosaurus maximus*, AMNH 5175, paratype, × 2; B, *Glyptosaurus rugosus*, AMNH 6055, × 2; C, *Arpadosaurus gazinorum*, n. gen., n. sp., holotype, × 2; D, *Peltosaurus granulosus*, KU 620, × 5; E, *Pancelosaurus piger*, n. gen., MCZ 3498, × 6 (Hell Creek Formation, Montana).

former two genera are also similar. This bone is essentially quadrangular in both of the above, while in *Melanosaurus* the same bone is more elongated.

The scutellation on the dorsal surface of the parietal of *Arpadosaurus* resembles much more that of *Melanosaurus* than of *Glyptosaurus*. In the first two genera, interparietal and occipital impressions are discernable; in *Glyptosaurus* the dorsal surface is covered by subequal polygonal plates.

The osteoscutal crust on the dorsal surface of the frontal bones of *A. gazinorum* is subdivided into unequal epidermal scute areas by numerous grooves; this surface is also irregular, featuring large depressed areas as well as elevated mounds. It is conceivable that further subdivisions of the osteoscutal crust could have led to the situation encountered in *Glyptosaurus*, in which numerous polygonal osteoscutal plates cover the frontal and other cranial bones.

Arpadosaurus gazinorum displays a number of features intermediate between *Melanosaurus* and *Glyptosaurus*, but since it occurs in strata of the same age as *Melanosaurus* and some glyptosaurs, *A. gazinorum* cannot at this time be regarded as anything more than a structural intermediate between the two genera. The origin of glyptosaurs perhaps lay in the Paleocene or very early Eocene.

Glyptosaurus Marsh 1871

Helodermoides Douglass 1903

Type species of the genus. Glyptosaurus sylvestris Marsh 1871.

Referred species. Glyptosaurus nodosus, G. rugosus, G. brevidens, G.? sphenodon, G. princeps, G. hillsi, G. obtusidens, and *G. donohoei* from the Eocene of North America; *G. montanus, G. giganteus*, and *G. tuberculatus* from the Oligocene of North America; *Glyptosaurus* near *nodusus* was recognized by Gilmore (1943) from the Eocene of Mongolia.

Geological range. Early Eocene to Oligocene of North America, Eocene of Mongolia, and questionably Paleocene to Eocene of Europe (see below).

Synopsis of known characters of the genus

The frontals, parietals, and the cheek region are covered by numerous polygonal osteoscutal plates. These cranial osteoscutes, as well as those of the body, are covered with raised tubercular mounds, which are often arranged in concentric patterns. The frontals are distinct or fused; in the latter case the point of fusion is generally marked by a raised ventral ridge. The palatines and pterygoids bear teeth. The postfrontals and prefrontals are narrowly separated above the orbit. The parietal foramen is present, and the postorbital is excluded from orbit formation. The body osteoscutes are rectangular, have a uniform width, and are much longer than wide. They are covered with tubercular mounds that are arranged in a concentric pattern. A deep groove is present between the smooth anterior gliding surface and the sculptured area. The gliding surface is an anterior transverse band and comprises about one-quarter of the total length of the osteoscutes. In every species some of the osteoscutes have feeble keels. Strongly jagged lateral edges indicate suturing between adjacent osteoscutes.

On the mandible the anterior extremities of the coronoid and surangular are in line on a vertical plane on the labial surface. The dentary reaches posteriad between the above two bones to the anterior supraangular foramen (Fig. 17b).

A survey of the glyptosaurs

Numerous polygonal plates sculptured with tubercular mounds cover the cranial elements as well as the cheek region in all the species of *Glyptosaurus*. These individual cranial plates may be rather flat, as in *G. hillsi, G. princeps*, and *G. sylvestris*, or strongly raised, forming a highly irregular

surface, as in *G. donohoei, G. giganteus, G. nodosus, G. rugosus,* and *G. tuberculatus.* These cranial osteoscutes tend to become larger in an anteroposterior direction (e.g. plates covering the parietal are larger than the ones on the frontal, and those covering the cheek region are even larger). The frontals are distinct in *G. sylvestris, G. nodosus, G. montanus,* and *G. tuberculatus.* These bones are fused but with a prominent suture line or a raised ridge marking the point of fusion, in *G. rugosus, G. hillsi, G. princeps,* and *G. giganteus.* In the other species the condition of the frontals is not determinable. The parietals are much shortened in *G. giganteus* and *G. montanus* relative to other species where this bone is known. In these same two species the frontals are also foreshortened, and postfrontals and prefrontals closely approach one another over the orbit. In *G. giganteus* the latter two bones are almost touching. In other species of *Glyptosaurus* prefrontals and postfrontals are moderately separated from one another.

Teeth in this genus range from the robust bulbous crushing teeth of *Glyptosaurus hillsi* (similar to the ones described and figured for *Arpadosaurus gazinorum*) to the recurved teeth with pointed unstriated apices of *G. tuberculatus* (similar to those of *Pancelosaurus pawneensis,* Pl. 1). *G.? sphenodon* has very slender teeth, and is much smaller than any of the other glyptosaurs; it is probably not a *Glyptosaurus.* The teeth in general are moderately heavy, with obtuse crowns that bear striations and an anteroposteriorly directed cutting edge. The largest members of this genus are *G. hillsi* and *G. giganteus.* The former probably had a slender and elongated head; in the latter the head was broad and relatively short. Both forms exceed by far the maximum size of any other known anguid. *G. nodosus* is the smallest glyptosaur. All species in which the mandible is known display the characteristic labial suturing between dentary and postdentary bones, in which the anterior extremities of the coronoid and surangular are on a vertical line (Fig. 17b), and the anterior inferior alveolar foramen is between the dentary and the splenial.

Discussion. The glyptosaurs are large lizards, some comparable in size to *Arpadosaurus* and *Melanosaurus,* while some (e.g. *G. giganteus* and *G. hillsi*) are much larger. The glyptosaurs are unique among anguids in that the head osteoscutes are broken up into numerous polygonal plates, resembling superficially in this respect the living *Heloderma.* These small bony osteoscutes are more loosely associated with the skull bones that they cover than is the case in many other anguids and consequently some are often missing. The polygonal plates, as well as the body osteoscutes, are covered with the same tubercular mounds as skull and body osteoscutes of *Melanosaurus, Arpadosaurus, Peltosaurus granulosus,* and *Xestops vagans.* This type of sculpture is not found in other fossil or Recent members of the Anguidae. The labial contact between the dentary and postdentary bones on the mandible is also nearly identical, in the glyptosaurs, to the latter four fossil genera further indicating that the affinities of glyptosaurs are with these forms. Osteoscutes of glyptosaurs are very similar to those of *Melanosaurus* and *Arpadosaurus* in respect to sculpture. general shape, strong lateral suturing, and in having a deep groove between the gliding surface and the sculptured area. As indicated earlier (p. 141), *Melanosaurus, Arpadosaurus,* and *Glyptosaurus,* respectively, can be placed in a structural series that may represent steps in the evolution of glyptosaurs from a more primitive *Melanosaurus*-like ancestor.

Several authors have suggested that the European *Placosaurus* is very close to *Glyptosaurus,* if not congeneric with it, and Romer (1967) lists *Glyptosaurus* as one of the synonyms for *Placosaurus.* Much of what is in the literature at present concerning this question is repetition of assumptions made by early workers. The generic

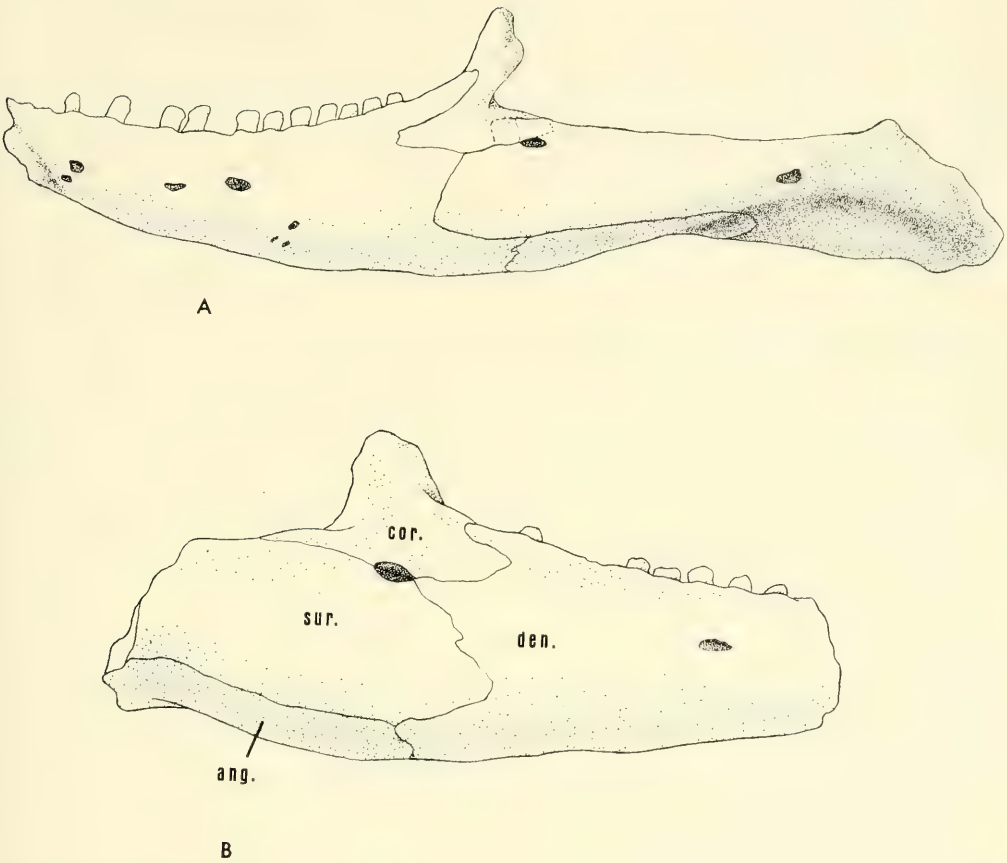

Figure 17. A, left mandible of *Peltosaurus granulosus, labial* view, FAM 42913; B, fragmentary right mandible of *Glyptosaurus, cf. G. obtusidens,* AMNH 5176. Note coronoid in advance of surangular in A, the two bones essentially in line in B; A × 3.3, B × 2.7.

name *Glyptosaurus* is retained here for the North American forms until actual study and comparison of the North American and European fossil forms is made.

THE SUBFAMILIES OF ANGUIDAE

The preceding discussion of fossil anguids gives a basis for evaluating the utility of anguid subfamilies based on modern forms. When the fossil record of the group is considered, it is difficult to list a series of characters that characterize the subfamilies, as will be seen below and as has been intimated frequently in the above review.

Anguinae. This group includes *Pancelosaurus,* the most primitive of known fossil anguids, and its limbless modern relatives *Anguis* and *Ophisaurus.* Because of the adaptive differences between the fossil and Recent forms, this subfamily is especially difficult to characterize, but all included forms share unfused frontals with well-separated frontoparietal epidermal scales, and a similar type of scutellation. *Anguis* has somewhat modified its scutes from the *Ophisaurus* condition (Fig. 6); the latter more closely resembles *Pancelosaurus,* gerrhonotines, and glyptosaurines in scute morphology. In the mandible, the sur-

angular and angular extend far forward of the coronoid in the Recent forms, slightly less so in *Pancelosaurus*. A premaxillary foramen is present in the Recent forms and probably, but not certainly, also occurred in *Pancelosaurus*. Vomers, palatines, and pterygoids are toothed in *Ophisaurus*, and at least the latter two bones were toothed in *Pancelosaurus* as well; palatal teeth are absent in *Anguis*.

Pancelosaurus was a limbed form, and was probably ancestral to the glyptosaurines; it also shows strong similarities to diploglossines and to gerrhonotines. It is close to the basal stock of known Anguidae.

Gerrhonotinae. Only the Recent genera *Gerrhonotus*, *Abronia*, and, perhaps, *Coloptychon* are included. This specialized group has fused, hourglass-shaped frontals, the frontoparietal scales almost or barely in contact on the midline, and lacks the premaxillary foramen of anguines and diploglossines. The forward extension of surangular and angular, and the type of scutellation, suggest that the group is derived from primitive limbed Anguinae.

Glyptosaurinae. This group includes only the extinct genera *Xestops*, *Peltosaurus*, *Melanosaurus*, *Arpadosaurus*, and *Glyptosaurus* (and their European relatives, for which synonymy is not yet clear). This subfamily possesses tuberculated osteoscutes, and the latter three genera show an increasing tendency to fragment the cephalic scutellation. The palate is toothed on palatines, and pterygoids in forms in which these bones are known. The premaxillary foramen is absent in *Peltosaurus*, but the condition in the other genera is not known; this character thus cannot be used to link *Peltosaurus* with the gerrhonotines. On the mandible, labial extensions of coronoid and surangular anteriorly are in a vertical plane except in *Peltosaurus*, which is anomalous in having the coronoid exceed the surangular.

This group is probably derived from *Xestops*, which is differentiated from the anguine *Pancelosaurus* mainly by its tuberculated osteoscutes. *Xestops* gave rise, probably, to the Oligocene *Peltosaurus*, in which the frontoparietal scales meet broadly on the midline. *Glyptosaurus*, the most extreme of the group in fragmentation of cephalic scutellation, was probably derived from *Xestops* through *Melanosaurus*-like and *Arpadosaurus*-like ancestors, and it lived through Oligocene time at least.

Diploglossinae. Only the Recent genera *Diploglossus* (including *Celestus* and *Sauresia*), *Ophiodes*, and *Wetmorena* are included here. This primitive group is distinctive, and has no fossil record outside of its present distribution in the West Indies. Cycloid scales with a peaked gliding surface distinguish them from all other anguids, although they are linked to the Anguinae by their separate frontals with well-separated frontoparietal scale impressions.

As might be expected, the fossil record thus shows intergradation between the rather well-defined Recent subfamilial groups. The resemblances of the fossil *Pancelosaurus* are primarily to the Anguinae; nevertheless, strong resemblances to the other subfamilies also occur.

Regardless of the intergradation shown above, the subfamily categories based on Recent forms may be maintained because they appear to represent actual lineages long established in the fossil record. The addition of the Glyptosaurinae is necessary, in addition, to encompass the Eocene-Oligocene radiation of forms with tuberculated osteoscutes.

SUMMARY AND CONCLUSIONS

The foregoing survey of the osteology and epidermal scalation of Recent Anguidae indicates that all extant forms fall into three groups worthy of subfamily status: (1) Anguinae (including *Ophisaurus* and *Anguis*), (2) Gerrhonotinae (including *Abronia*, *Gerrhonotus*, and possibly *Coloptychon*), (3) Diploglossinae (including *Diploglossus*, *Wetmorena*, and *Ophiodes*). All these extant forms, excepting the ger-

rhonotines (*Abronia* and *Gerrhonotus*), have paired frontal bones and a premaxillary foramen (see Fig. 2). This foramen is restricted, among Recent lizards, to the genera *Ophisaurus, Anguis, Diploglossus, Wetmorena,* and *Ophiodes.* It may possibly have been present in the fossil genus *Pancelosaurus,* but its presence in other fossil forms cannot be determined except in *Peltosaurus,* in which it is absent. These characters clearly set the Gerrhonotinae apart from the other Recent anguids, but gerrhonotines do share a similar body scutellation and a lateral fold with the ophisaurs. In this respect the Diploglossinae, with their unique (in anguids) cycloid body osteoscutes, stand apart from the rest of the Recent forms.

The anguines, sharing some characters with both, appear to be structurally intermediate between the Gerrhonotinae and the Diploglossinae. They are primitive (except for *Anguis*) in regard to their toothed pterygoids and palatines (and vomers in some), although Recent forms are limbless.

Anguis shares a great number of osteological as well as scalation characters with *Ophisaurus* (see page 101), differing from this genus only in characters judged here to be degenerate: (1) reduced interclavicle; (2) complete absence of palatal teeth; (3) thin, feebly-developed osteoscutes with the anterior gliding surface reduced so as to become confluent with the lateral bevel; (4) absence of a lateral fold, a feature apparently correlated with the reduction of the body armor; (5) absence of an external ear opening (a condition also found in some *Ophisaurus*). *Anguis* appears to be a degenerate ophisaur derived from a limbless *Ophisaurus* ancestor.

In the North American fossil record, fossil remains unquestionably those of lizards of the family Anguidae first occur in late Cretaceous sediments of Wyoming and Montana. This anguid, formerly known as *Peltosaurus piger,* was first described by Gilmore (1928) on the basis of two jaw elements. The generic assignment was based on a tooth structure similar to that of the Oligocene *Peltosaurus granulosus.* This early anguid is here placed in a new genus, *Pancelosaurus,* based on study of a large number of previously unknown cranial elements recovered through washing and screening methods.

The cranial elements of *Pancelosaurus piger,* in their close resemblance to those of some Recent genera (*Ophisaurus, Gerrhonotus, Diploglossus*), point to the fact that most of the Eocene and Oligocene fossil anguids represent a side line of anguid evolution rather than being ancestors of the Recent forms (see below). *Pancelosaurus piger* exhibits a mosaic of characters in its skeleton, showing some resemblance to each of the above Recent genera, especially *Ophisaurus.* Since its body osteoscutes most closely resemble those of *Gerrhonotus* and *Ophisaurus,* perhaps this Cretaceous form was already specialized toward the line leading to these two Recent genera. It exhibits many of the same primitive and intermediate characters between the diploglossines and the gerrhonotines as do the ophisaurs and is regarded here as a primitive limbed member of the Anguinae.

Pancelosaurus piger is known from late Cretaceous through late Paleocene deposits. The genus extends into the middle Oligocene as *P. pawneensis* (formerly *Xestops pawneensis*). *Pancelosaurus* is the only fossil anguid in late Cretaceous and Paleocene deposits of North America that is known to such an extent as to allow for generic diagnosis. *Peltosaurus jepseni,* described by Gilmore, is a synonym of *P. piger.*

The large Eocene and Oligocene fossil forms such as *Xestops, Peltosaurus, Melanosaurus, Arpadosaurus,* and *Glyptosaurus* may also have been derived from *Pancelosaurus* or its relatives, as is indicated by similar body osteoscutes. These are more robust than those of *P. piger* and contrast with those of the latter in being covered

with tubercular mounds. This sculpture type is found only in the above Eocene and Oligocene forms, and combined with a characteristic pattern of labial suturing between dentary and postdentary bones, indicates their distinctness from other anguids. They are placed here in the extinct subfamily Glyptosaurinae. In this concept of the glyptosaurines, the Eocene species *Xestops vagans* appears to be the most primitive form, sharing some primitive characters of the frontal bones with *P. piger,* while exhibiting the above-mentioned glyptosaurine characters. *Dimetopisaurus wyomingensis* is a synonym of *Xestops vagans.*

All the known North American genera referable to the Glyptosaurinae occur in deposits only of Eocene (*Arpadosaurus, Glyptosaurus, Melanosaurus,* and *Xestops*) or Oligocene (*Glyptosaurus* and *Peltosaurus*) age. However, three large, keeled body osteoscutes bearing the diagnostic tubercular sculpture of the Glyptosaurinae have been reported by Estes and Tihen (1964) from the Mio-Pliocene Valentine Formation of Nebraska. Unless they are reworked, these scutes indicate that some unknown glyptosaurine survived until the late Miocene or early Pliocene.

In the Glyptosaurinae, the new genus *Arpadosaurus* appears to be structurally intermediate between *Melanosaurus* and *Glyptosaurus,* and it is postulated that the glyptosaurs may have originated from a form like *Melanosaurus;* more evidence is needed to confirm this hypothesis, however.

It is postulated above that *Pancelosaurus piger* or a closely related form may have given rise to both the extant ophisaurs and gerrhonotines or only to the former. There is indeed nothing in the known anatomy of *P. piger* that would contradict such an assumption, but in the absence of a more complete fossil record, the origin of these Recent forms is still hypothetical.

The only fossil form referred to the Gerrhonotinae and consisting of more than jaw elements is *Paragerrhonotus ricardensis* (Estes, 1964) from the early Pliocene of California. This fossil form poses more problems than it solves. Although frontal bones are fused and display strongly emarginate concave borders as in the Recent *Gerrhonotus,* the osteoscutal crust on the frontal is broken up into several facets instead of exhibiting the usual epidermal imprints of Recent anguids. This is a trend often seen in anguimorphs (cf. *Parasaniwa, Glyptosaurus, Exostinus, Heloderma*). It is probably a specialized sideline, derived from *Gerrhonotus.*

Estes (1964) regarded some anguid dentaries from the Lance Formation as near *Gerrhonotus.* These jaw fragments with *Gerrhonotus*-like teeth occur in the same deposits as *Pancelosaurus piger.* No other cranial elements have been recovered. Without the presence of the specialized frontals of *Gerrhonotus* (or a closely allied form) in the Cretaceous, its presence cannot be confirmed, and it is also possible that these jaw fragments may represent a smaller species of *Pancelosaurus.*

Gerrhonotus-like jaws were also noted by McKenna (1960) from the Eocene (Wasatchian) Four Mile local fauna of Colorado, and the Mio-Pliocene Valentine Formation of Nebraska (Estes and Tihen, 1964). These identifications, like those from the Lance Formation, are not supported so far by any other cranial elements.

Remains of ophisaurs referable to or close to Recent species have been described both from the Pliocene of Europe and from the Pleistocene and Pliocene of North America, and Młynarski (1960, 1964) described the remains of *Ophisaurus pannonicus* from the early Pliocene of Poland. He regarded this form as very close to if not conspecific with *Ophisaurus apodus.* From these same deposits Młynarski (1964) described the remains of *Anguis* cf. *fragilis.* Etheridge (1960) recognized the extant *O. attenuatus* as early as the late Pliocene of Kansas. Auffenberg (1955) recognized both *O. ventralis* and *O. compressus* from

the Pleistocene of Florida. Thus it appears that establishment of the Recent species of *Ophisaurus* had begun at least by the beginning of the Pliocene, and that *Anguis* was distinct from the ophisaurs by that time.

The middle Eocene European Geiseltal deposits contain numerous anguid fossils; some were said by Kuhn (1940) to show resemblance to the ophisaurs. I have not seen this material, and Kuhn's figures are poor, but study of this material will shed some more light on the phylogeny of the Anguinae as here constituted, as well as on that of the Anguidae in general.

The diploglossines have no fossil record beyond Pleistocene cave finds (Etheridge, 1964, 1965).

The preceding account illustrates the incomplete state of the fossil record of the Anguidae, especially that of the Recent forms, and also the need for new discoveries, as well as reworking of existing fossil material.

Some of the main conclusions reached by this investigation may be summarized as follows:

(1) The Recent anguids and the North American fossil forms fall into four groups worthy of subfamily status: (1) Anguinae, (2) Diploglossinae, (3) Gerrhonotinae, (4) Glyptosaurinae. The Diploglossinae, in many ways primitive, has essentially no fossil record; the Glyptosaurinae is extinct.

(2) The Glyptosaurinae (*s.l.*) contains most of the well-known fossil anguids (*Glyptosaurus, Melanosaurus, Peltosaurus,* and *Xestops*) and a new genus, *Arpadosaurus.*

(3) The glyptosaurines appear in the early Eocene of North America and disappear from the fossil record by or just before the beginning of the Pliocene.

(4) *Peltosaurus,* long considered a close relative of *Gerrhonotus,* is shown to have a greater resemblance to the glyptosaurines (especially *Xestops*).

(5) The earliest known anguid is *Pancelosaurus piger* from the late Cretaceous of Wyoming and Montana. This is the only anguid fossil in Cretaceous and Paleocene deposits of North America that is known to such an extent as to allow generic diagnosis. A related species, *P. pawneensis,* occurs in the Oligocene of Wyoming.

(6) *Pancelosaurus piger* displays a body scutellation similar to that of *Gerrhonotus* and *Ophisaurus,* and this early fossil appears to be already a member of the Anguinae, but the imperfect fossil record prevents more positive statements concerning the phylogeny of the above Recent forms.

Abbreviations

a = angular
aaf = anterior inferior alveolar foramen
ain = anterior internasal epidermal scale
amf = anterior mylohyoid foramen
asf = anterior supra-angular foramen
c = coronoid
d = dentary
e = ectopterygoid
fn = frontonasal epidermal scale
fp = frontoparietal epidermal scale
fr = frontal epidermal scale
ip = interparietal epidermal scale
m = maxilla
oc = occipital epidermal scale
pa = parietal epidermal scale
part = fused articular and prearticular
pf = premaxillary foramen
pfr = prefrontal epidermal scale
pin = posterior internasal scale
pl = palatine
pm = premaxilla
pt = pterygoid
r = rostral epidermal scale
sa = surangular
so = supra-orbital epidermal scale
sp = splenial
v = vomer

LITERATURE CITED

Auffenberg, W. 1955. Glass lizards (*Ophisaurus*) in the Pleistocene and Pliocene of Florida. Herpetologica **2** (2): 133–136.

Barrows, S., and H. M. Smith. 1947. The skeleton of the lizard *Xenosaurus grandis* (Gray). Univ. Kansas Sci. Bull. **31:** 227–281.

Bogert, C. M., and A. P. Parker. 1967. A new species of *Abronia* (Sauria, Anguidae) from

the Sierra Madre del Sur of Oaxaca, Mexico. Amer. Mus. Novit. No. **2279**: 1–21.

Boulenger, G. A. 1885. Catalogue of the Lizards in the British Museum (Natural History). Vol. II, 2nd ed., London, xii + 497 pp.

——— 1918. Les lézards hélodermatides de l'Éocène supérieur de la France. C. R. Acad. Sci. Paris. **166**: 1–4.

Burt, C. E., and M. C. Burt. 1931. South American lizards in the collection of the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. **61**: 227–395.

Camp, C. L. 1923. A classification of the lizards. Bull. Amer. Mus. Nat. Hist. **48**: 289–481.

Cope, E. D. 1864. On the characters of the higher groups of Reptilia, Squamata and especially of the Diploglossa. Proc. Acad. Nat. Sci. Philadelphia **1864**: 224–231.

——— 1873. Second notice of extinct Vertebrata from the Tertiary of the Plains. Paleont. Bull. **15**: 5–6.

——— 1884. The Vertebrata of the Tertiary formations of the West. Rep. U. S. Geol. Surv. Terr. (Hayden) **3**: 770–781.

——— 1900. The crocodilians, lizards and snakes of North America. Rep. U. S. Nat. Mus. **1898**: 153–1294.

Criley, B. B. 1968. The cranial osteology of gerrhonotiform lizards. Amer. Midl. Nat. **80**: 199–219.

Darlington, P. J., Jr. 1957. Zoogeography: the Geographical Distribution of Animals. New York, Wiley and Sons, xi + 675 pp.

Douglass, E. 1903. New vertebrates from the Montana Tertiary. Ann. Carnegie Mus. **2**: 145–199.

——— 1908. Some Oligocene lizards. Ann. Carnegie Mus. **4**: 278–281.

Estes, R. 1963a. Early Miocene salamanders and lizards from Florida. Quart. J. Florida Acad. Sci. **26**: 234–256.

——— 1963b. A new gerrhonotine lizard from the Pliocene of California. Copeia **1963** (4): 676–680.

——— 1964. Fossil vertebrates from the late Cretaceous Lance Formation, Eastern Wyoming. Univ. Calif. Publ. Geol. Sci. **49**: 1–180.

Estes, R., P. Berberian, and C. A. M. Mezoely. 1969. Lower vertebrates from the late Cretaceous Hell Creek Formation, McCone County, Montana. Breviora, Mus. Comp. Zool., **337**: 1–33.

Estes, R., and J. A. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. Amer. Midl. Nat. **75**: 495–515.

Etheridge, R. 1960. The slender glass lizard, *Ophisaurus attenuatus*, from the Pleistocene (Illinoian Glacial) of Oklahoma. Copeia **1960** (1): 46–47.

——— 1961. Late Cenozoic glass lizards (*Ophisaurus*) from the southern Great Plains. Herpetologica **17**: 179–186.

——— 1964. Late Pleistocene lizards from Barbuda, British West Indies. Bull. Florida State Mus. **9**: 43–75.

——— 1965. Fossil lizards from the Dominican Republic. Quart. J. Florida Acad. Sci. **28**: 83–105.

Gazin, C. L. 1956. Paleocene mammalian faunas of the Bison Basin in south-central Wyoming. Smithsonian Misc. Coll. **131** (6): iv + 57 pp.

——— 1962. A further study of the Lower Eocene mammalian faunas of southwestern Wyoming. Smithsonian Misc. Coll. **144**: 1–98.

Gervais, P. 1859. Zoologie et Paléontologie Françaises. 2nd Ed. Paris, 543 pp.

Gilmore, C. W. 1928. Fossil lizards of North America. Mem. Nation. Acad. Sci. **22**: ix + 201 pp.

——— 1938. Description of new and little-known fossil lizards from North America. Proc. U. S. Nat. Mus. **86**: 11–26.

——— 1942. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Part II: Lizards. Proc. Amer. Philos. Soc. **85**: 159–167.

——— 1943. Fossil lizards of Mongolia. Bull. Amer. Mus. Nat. Hist. **81**: 361–384.

Hecht, M. K. 1959. Amphibians and reptiles. *In*: McGrew, P. O., The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Amer. Mus. Nat. Hist. **117**: 130–146.

Hoffstetter, R. 1962a. Observations sur les osteodermes et la classification des anguides actuels et fossiles (Reptiles, Sauriens). Bull. Mus. Nat. Hist. Nat. **34**: 149–157.

——— 1962b. Additions à la faune reptilienne de l'Éocene supérieur de Mormont-Saint-Loup (Suisse). Bull. Soc. Géol. France (7) **4**: 109–117.

Holman, J. A. 1958. The Pleistocene herpetofauna of Saber-tooth Cave, Citrus County, Florida. Copeia **1958** (4): 276–280.

——— 1965. A new glass lizard from Veracruz, Mexico. Quart. J. Florida Acad. Sci. **27** (2): 311–315.

Kuhn, O. 1940. Die Placosauriden und Anguiden aus dem Mittleren Eozän des Geiseltales. Nova Acta Acad. Leop.-Carol. **53** (8): 461–486.

Marsh, O. C. 1871. Notice of some new fossil reptiles from Cretaceous and Tertiary formations. Amer. J. Sci. **3** (1): 447–459.

——— 1872. Preliminary description of new Tertiary reptiles, part 1. Amer. J. Sci. **4**: 298–309.

McConkey, E. H. 1954. A systematic study of the North American lizards of the genus *Ophisaurus*. Amer. Midl. Nat. **51** (1): 133–174.

——— 1955. A new lizard of the genus *Ophisaurus* from Mexico. Nat. Hist. Misc., Chicago Acad. Sci. **145:** 1–2.

McDowell, S. B., and C. M. Bogert. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. Bull. Am. Mus. Nat. Hist. **105** (1): 1–145.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile fauna, Eocene of northwest Colorado. Univ. Calif. Publ. Geol. Sci. **37:** 1–130.

——— 1962. Collecting small fossils by washing and screening. Curator **5:** 221–235.

Młynarski, M. 1960. Pliocene amphibians and reptiles from Rebielice Krolewskie (Poland). Acta Zool. Cracov. **5** (4): 131–150.

——— 1964. Die jungpliozäne Reptilien-fauna von Rebielice Krolewskie, Polen. Senck. Biol. Frankfurt a.M. **45:** 325–347.

Romer, A. S. 1956. Osteology of the Reptiles. Chicago, Univ. Chicago Press, xxi + 772 pp.

——— 1967. Vertebrate Paleontology. 3rd Ed., Chicago, Univ. Chicago Press, viii + 468 pp.

Sloan, R., and L. Van Valen. 1965. Cretaceous mammals from Montana. Science **148:** 220–227.

Stebbins, R. C. 1958. A new alligator lizard from the Panamint Mountains, Inyo County, California. Amer. Mus. Novit. No. **1883:** 1–27.

Tihen, J. A. 1949. The genera of gerrhonotine lizards. Amer. Midl. Nat. **41** (3): 580–601.

——— 1949. A review of the lizard genus *Barisia*. Univ. Kansas Sci. Bull. **33** (3): 217–256.

——— 1954. Gerrhonotine lizards recently added to the American Museum collection with further revisions of the genus *Abronia*. Amer. Mus. Novit. No. **1687** (4): 1–26.

Underwood, G. 1959. A new Jamaican galliwasp (Sauria, Anguidae). Breviora, Mus. Comp. Zool., No. **102:** 1–13.

——— 1964. An anguid lizard from the Leeward Islands. Breviora, Mus. Comp. Zool., No. **200:** 1–10.

Vanzolini, P. E. 1952. Fossil snakes and lizards from the Lower Miocene of Florida. J. Paleon. **26:** 452–457.

White, T. E. 1952. Preliminary analysis of the vertebrate fossil fauna of the Boysen Reservoir area. Proc. U. S. Nat. Mus. **102:** 185–207.

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A Subfamilial Classification of Scincid Lizards

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Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

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A SUBFAMILIAL CLASSIFICATION OF SCINCID LIZARDS

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ABSTRACT

The subfamilial classification of skinks which is proposed is based primarily on the osteology of the skull, particularly on the relationships of the bones of the secondary palate and the frontal bones, and on external morphology. These, plus other characters important in understanding the evolution and classification of the higher taxa of skinks, are discussed in some detail.

Four subfamilies are recognized. The Scincinae (approximately 28+ genera and 182 species) are considered to be the most primitive subfamily of skinks and are apparently independently ancestral to the other three subfamilies. The scincines occur in Asia and Africa, and in the New World north of Costa Rica (*Eumeces* and *Neoseps*), but are conspicuously absent from the Australian Region. The center of abundance and diversity of scincines today is in subsaharan Africa and the islands of the western Indian Ocean. The Feylininae (2 genera and 4 species) and Acontinae (3 genera and 15 species) are specialized burrowing taxa which almost surely evolved independently from the scincines of subsaharan Africa where both subfamilies are confined today. The fourth subfamily, the Lygosominae (appoximately 40+ genera and 600+ species), is the most numerous and diverse subfamily of skinks. They appear to have arisen from a scincine ancestry and have radiated spectacularly in the Australian Region and southeast Asia. From this area, they have spread west into Africa and across the Atlantic into the New World (*Mabuya*), and north and east across a Bering Straits land bridge into North and Central America (*Leiolopisma*). It is suggested that the radiation and expansion of the lygosomines is responsible in part for the apparent decline of the scincines in certain areas such as Asia.

INTRODUCTION

The only attempt at a suprageneric classification of skinks was provided by Mittleman (1952) as a kind of preface to his synopsis of the genera that are related to or often grouped under (as subgenera) the catch-all genus *Lygosoma*. The four subfamilies recognized were diagnosed by means of a key, and the general distribution of each subfamily was given. Only the genera of the subfamily Lygosominae, however, received further attention.

Mittleman's (1952) diagnostic key to the four subfamilies of skinks is as follows:

A. Palatine bones in contact on median line of palate.
   1. Pterygoid bones separated on the median line of palate; palatal notch extending anteriorly to level of centers of eyes ..... MABUYINAE.
   2. Pterygoid bones in contact anteriorly; palatal notch not extending anteriorly to level of centers of eyes ..... LYGOSOMINAE.

B. Palatine bones separated on median line of palate.

1. Nostril pierced in nasal, or between two adjacent plates, but never touching rostral ..... SCINCINAE.
2. Nostril pierced between rostral and adjacent plate, thereby contacting rostral, or else within rostral itself ..... CHALCIDINAE.

In the course of my research on the supraspecific relationships of skinks, I have attempted to correlate skull osteology with external morphology in delimiting taxa. This study, which is based on data from the complete skulls of over 350 species of skinks, has suggested to me a subfamilial classification that has a sounder basis than that of Mittleman.

Mittleman's (1952) diagnoses of the three subfamilies Mabuyinae, Scincinae, and Chalcidinae are accurate descriptions of three possible assemblages of skinks, but none of these assemblages can be defended as a monophyletic unit. This should become evident in the discussion of the new classification. Mittleman's diagnosis of the Lygosominae, on the other hand, constitutes an inaccurate description of many of the genera which he included in the group, but his generic list for the subfamily includes most of the genera that I believe should constitute a subfamily Lygosominae. The Lygosominae of Mittleman is, in other words, an inaccurately diagnosed but well conceived taxonomic group.

In his characterization of the Lygosominae, Mittleman (1952) fell into the same trap as did Boulenger (1887) and M. A. Smith (1935) in their skink classifications. All three authors attempted to interpret the important relationships of the bones of the palate without removing the overlying buccal mucosa. In several lygosomine genera the pterygoids (i.e., their palatal rami) are completely separated along the midline by the interpterygoid vacuity or by processes that project posteriorly from the palatines. Thus not only does the type species of the type genus of the subfamily Lygosominae, *Lygosoma quadrupes*, disagree with Mittleman's diagnosis of the subfamily, but the following genera do as well: *Ablepharus, Cryptoblepharus, Emoia, Eumecia, Eugongylus, Leiolopisma* (part), *Leptosiaphos, Riopa* (part), *Siaphos* (part), and *Sphenomorphus* (part).

The four subfamilies in the classification proposed below are each based on the correlation of several skull and external characters, rather than on a single skull or external character, as were Mittleman's (1952) subfamilies, and the resulting distribution of the subfamilies is more meaningful zoogeographically than was Mittleman's arrangement.

CHARACTERS UTILIZED

Before discussing the four subfamilies of skinks, it will be worthwhile to review briefly some of the characters that have been most useful in diagnosing the higher taxa of skinks. This discussion will be limited to the taxonomic use of these characters, as the phylogenetic significance of these and other characters will be considered in a later section of the paper.

Secondary palate. Apart from *Dibamus* and *Anelytropsis*, which appear to be related to one another but whose relationships with other lizards are obscure (Miller, 1966b), skinks are the only family of lizards with a bony secondary palate. The secondary palate may be complete or incomplete depending on the degree of apposition (meeting along the midline or not, respectively) of the horizontal lamellae of the palatine bones. As a further advance-

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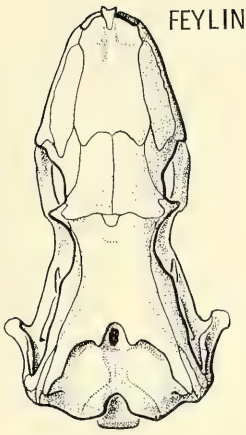
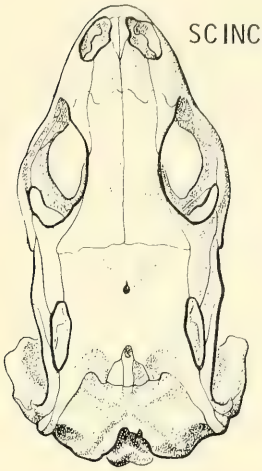
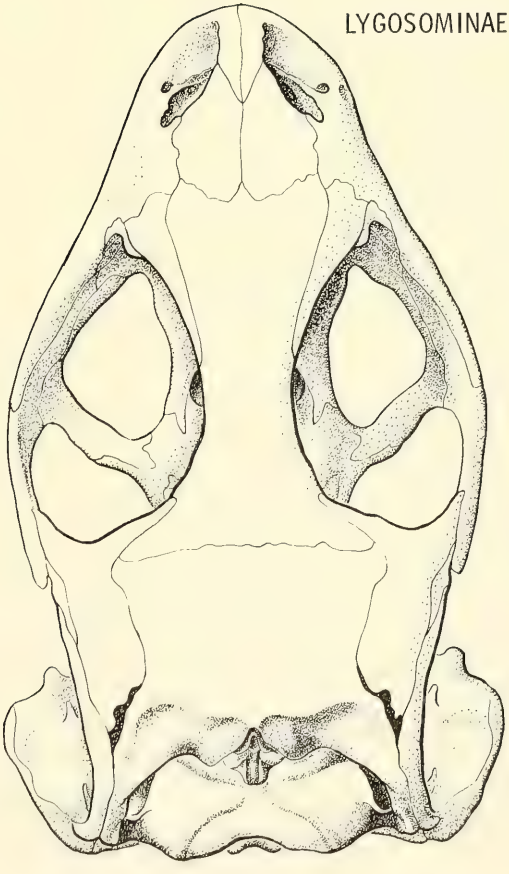
Figure 1. Dorsal view of the skulls of representatives of the four subfamilies of skinks. Feylininae: *Feylinia polylepis* (MCZ 61215); Scincinae: *Proscelotes arnoldi* (MCZ 55145); Acontinae: *Acontias breviceps* (MCZ 38559); Lygosominae: *Sphenomorphus jobiensis* (BM 1935.5.10.108). Drawn to scale.


FEYLININAE


SCINCINAE

ACONTINAE


LYGOSOMINAE

ment on the complete secondary palate, the palatal rami of the pterygoids may also meet along the midline with the palatines to make an even more extensive secondary palate.

The secondary palate is a diagnostic feature of skinks as a family, and the complex relationships, as well as shapes, of the bones forming the palate (and those bordering it) are useful in recognizing subfamilies and taxa of lower rank (Greer, 1967a and b; Greer and Parker, 1968).

Osteoderms. The second partially diagnostic feature of skinks as a family is the characteristic arrangement of the tubules in the osteoderms, i.e., an approximately transverse canal with anteriorly and posteriorly projecting longitudinal canals (see Gosse, 1848; Duméril and Bocourt, 1881; Otto, 1908; Hewitt, 1929; Smith, 1935; Sibtain, 1938; Ali, 1947; Oliver, 1951; Fitch, 1954; Ganapati and Rajyalakshmi, 1958; Deraniyagala, 1960; Tilak and Rastogi, 1964, and Rathore, 1967 for figures of skink osteoderms).

A similar pattern of tubules is found in some gerrhosaurine osteoderms and serves to align this subfamily of cordylids with skinks.

Hewitt (1929) has sought to use the number of "cells" created by the radiating osteoderm tubules as a means of working out the relationships of major groups of skinks. No one has followed Hewitt's lead, but it might be profitable to do so in the future.

Frontal bones. The separation or fusion of the frontal bones correlates well with certain relationships of the bones in the secondary palate and is important in diagnosing the four subfamilies of skinks. The condition of the frontal is, of course, also an important character in diagnosing major taxa in other lizard families.

Nasal bones. These bones are fused in one subfamily (Feylininae) and distinct in the other three. Given the great number and diversity of species in these latter three subfamilies, the fusion of the nasals in one group of skinks is important.

Ectopterygoid. This bone can show a good deal of variation in its relationships with the bones (palatine and pterygoid) of the secondary palate. These relationships are important at the subfamily level and below.

Jugal. This bone is lacking in one small subfamily (Feylininae), and, as it is lacking in only two other very closely related genera of skinks, its loss is an important feature.

Teeth. The presence or absence of pterygoid teeth and the number of premaxillary teeth seem to correlate well with other characters of taxa at the level of genus or species group. In general, these two characters, especially the number of premaxillary teeth, seem to be of greater taxonomic significance in skinks than in most other lizard families.

Supratemporal arch. Skinks are often diagnosed as displaying a complete supratemporal arch, that is, the postfrontal and squamosal bones articulate with one another either directly or through a postorbital bone. This is true in three of the subfamilies of skinks, the Feylininae, Scincinae and Lygosominae, but it is not true in the fourth subfamily, the Acontinae (with the exception of two species). In this last group the postfrontal and squamosal are generally small (a postorbital is lacking) and do not form a complete arch.

Meckel's groove. Meckel's groove may either be open anterior to the splenial or be closed by the overlapping and fusion of the dentary. There are only a few species with an intermediate condition (dentary overlapping but not fused along the resulting suture), and either one condition or the other seems to be characteristic of major groups of skinks.

External naris. In two of the four subfamilies (Feylininae and Acontinae) the external naris is situated in a large, posteriorly expanded rostral, and in the lygosomines the naris is in a discrete nasal

scale. The Scincinae, however, show a variety of relationships between the external naris and the surrounding scales; these relationships are of some value in recognizing the taxa within this group.

Preanal scales. The single, transverse preanal scale in one subfamily (Acontinae) is unique among skinks, with the exception of a few species of *Tropidophorus*, and is unusual in lizards. The size of the preanal scales relative to one another and to the posterior ventral scales is a useful character for aligning major groups of lygosomine skinks.

Appendages. The relative frequency of the species that have completely lost the external appendages in the four subfamilies reflects, to some extent, the degree to which the subfamilies have "gone underground," that is, have become burrowers.

Length of tail. The relatively short tails (less than one-third of the total length) of two of the subfamilies (Feylininae and Acontinae) might be thought of simply as an adaptation to a burrowing way of life, but the burrowers of the other two subfamilies have the relatively longer tails characteristic of their groups.

Mode of reproduction. The two smallest subfamilies, the Feylininae and the Acontinae, seem to be live-bearing, whereas the two larger subfamilies, the Scincinae and Lygosominae, are both egg-laying and live-bearing. Since egg-laying habits are undoubtedly ancestral to live-bearing habits, this character helps to establish the possible phylogeny of the four subfamilies.

THE SUBFAMILIES OF SKINKS

The four subfamilies discussed below are not arranged in any phylogenetic order, as is often the case in papers of this nature. Instead, the two small (in terms of number of species) and highly specialized subfamilies, the Feylininae and Acontinae, are discussed first; the Scincinae, which are considered to be independently ancestral to all three other subfamilies, come next and are followed by the Lygosominae, the most numerous, diverse, and advanced group of skinks.

In the description of the skull features of the four subfamilies, only the taxonomically important characters will be considered. The bones of the secondary palate are described in detail first, as they offer the most diagnostic characters for recognizing the subfamilies. The remainder of the bones of the skull are then described in a generally anterior-posterior order. The teeth and mandible are described last.

Feylininae

Diagnosis. Frontal bones separate (Fig. 1); premaxillae and nasal bones fused. Horizontal laminae from lateral sides of palatines approaching but not touching on ventral midline. An anteriorly projecting process from palatal ramus of pterygoid articulates with maxilla to exclude palatine from position on medial edge of infraorbital vacuity (Fig. 2).

Post-temporal fenestra reduced in size; supratemporal arch complete, i.e., postfrontal articulates with squamosal, which is closely applied to parietal. Postorbital and jugal bones lacking. Lateral descending processes from frontals and parietal fingerlike, i.e., not expanded.

Bony shaft of stapes abutting directly against quadrate.

Seven teeth on premaxillae; 13–14 teeth on maxilla.

Meckel's groove open anterior to splenial.

Rostral and mental scales slightly enlarged. External naris connected with posterior edge of rostral by short suture. Limbs totally lacking. Preanal scales not enlarged, i.e., approximately same size as other ventral, posterior body scales.

Description of skull. Cope (1892) has figured and described certain features of the skull of *Feylinia currori*. The following account is based on the skulls of two species, *Feylinia polylepis* and *F. currori*. The skulls of both species are very similar.

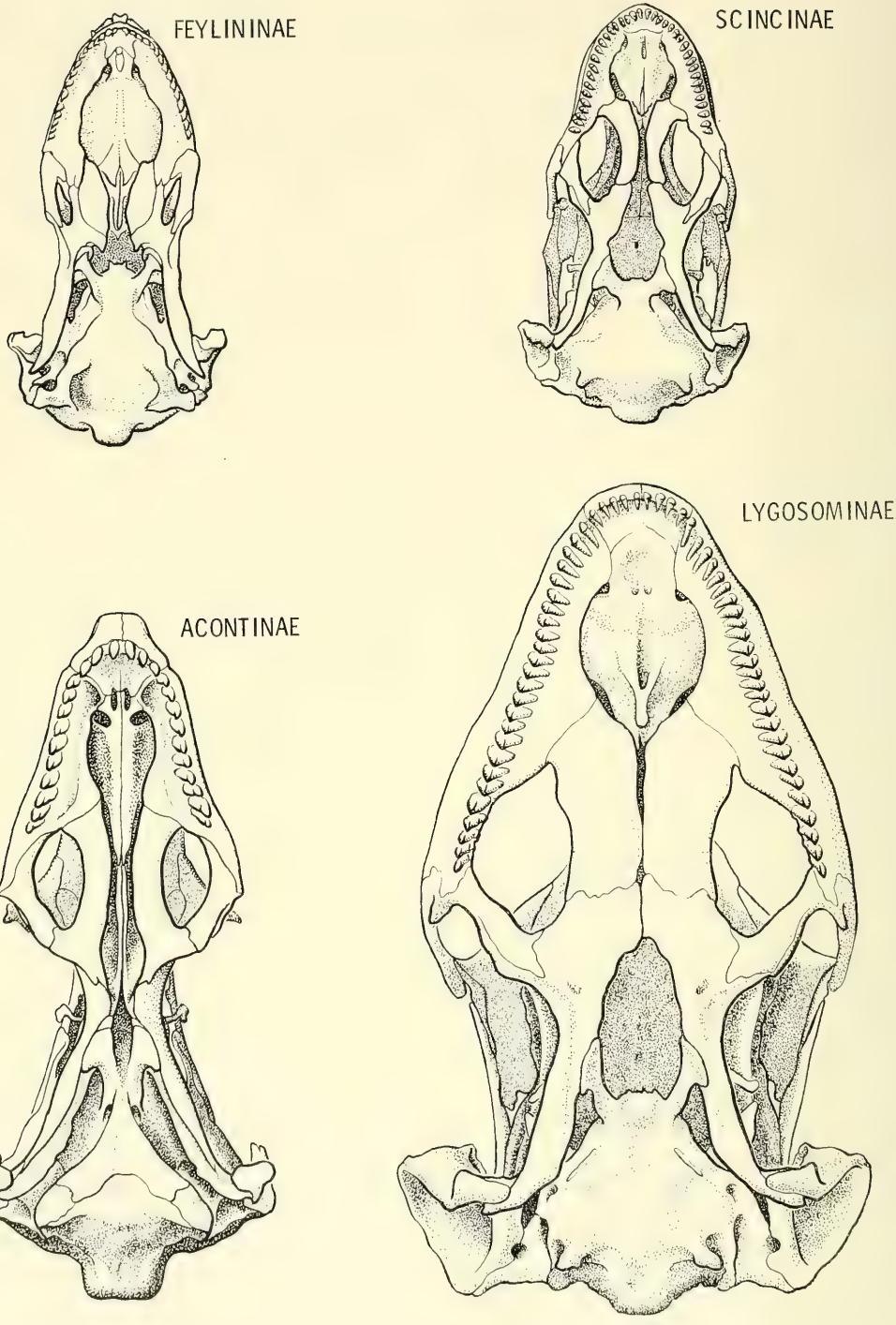


Figure 2. Ventral view of the skulls of representatives of the four subfamilies of skinks. Same species as represented in Figure 1 except for the Acontinae, which are represented by *Acontias meleagris* (MCZ 11934). Drawn to scale.

The skull as a whole is somewhat depressed for its length, and the postorbital region is not as elongate as might be expected in a lizard so obviously adapted to a burrowing existence.

The palatines are scroll-like, with the two free edges of each "scroll" just failing to meet medioventrally. Each palatine thus forms a separate air passage, with the ventral surfaces of the palatines acting as a rudimentary secondary palate to partially separate the food and air passages. The palatal rami of the pterygoids are separated medially and therefore do not participate in the formation of the secondary palate.

The palatal ramus of the pterygoid articulates with the ectopterygoid along the posterior edge of the infraorbital vacuity and sends an anterior process forward to the maxilla to exclude the palatine from a position on the medial edge of the infraorbital vacuity (Fig. 2).

The premaxillae, vomers, and nasals are each fused to form single elements, but the frontal is paired. The parietal is single and anteriorly bears a foramen, which, however, is overgrown by a bony boss on the dorsal surface.

The prefrontal is very large and occupies most of the anteromedial side of the orbital area. On the dorsal surface of the skull, the prefrontal articulates with the nasal. The suborbital bar is composed entirely of the ectopterygoid and an articulating process from the palatal ramus of the pterygoid. A jugal (postorbital bar) is lacking. The postfrontal bone is small and compact.

There is a single pair of thin, fingerlike, lateral processes descending from both the frontals and parietal. Those from the frontal are closely applied to the prefrontal and curve inward toward the midline but do not meet to encircle the forebrain. The processes from the parietal hang free and touch only the dorsally projecting epipterygoid. These parietal processes are similar to those of most non-burrowing lygosomine skinks and are not in the least expanded into long processes such as those which enclose most of the hindbrain of such typical burrowers as the Acontinae.

There is a small post-temporal fenestra, but although the supratemporal arch is complete, the supratemporal fenestra is obliterated by the close apposition of the squamosal to the parietal. A postorbital bone is absent.

The quadrate is short and stout, with a vertical ridge on its anterior surface. A horizontal, posteriorly projecting process with a ventral, terminal inflection arises from the posterodorsal surface of the quadrate. The footplate of the stapes is large, and the bony shaft abuts against the inner side of the ventral inflection of the posterior process of the quadrate.

Posteriorly curved, almost fanglike teeth are present on the fused premaxillae, maxillae, and dentaries. There are no teeth on any of the other bones of the skull or jaw. Both species of *Feylinia* examined possess seven teeth on the fused premaxillae and 13–14 teeth on the maxilla.

The skull and mandible lack pigment.

In the lower jaw, the articular, prearticular, and surangular are fused. The angular is reduced in size. The splenial extends posteriorly to occupy much of the position held by the angular in other skinks. The coronoid process is low, and Meckel's groove is present.

Description of external characters. The single rostral and mental scales are slightly enlarged; the external naris lies within the rostral and is connected with the posterior edge of the rostral through a short horizontal or curved suture. The middorsal head scales consist of a pair of postrostral scales (in *Feylinia*) or a single postrostral scale (in *Chabanaudia*), and following this, three single, large, median scales.

An external ear opening is lacking. The body scales are smooth and disposed in 16–30 longitudinal rows at midbody. The preanal scales are subequal with the other ventral, posterior body scales.

Limbs are absent, although rudimentary

pectoral and pelvic girdles are present (Essex, 1928). The tail is relatively short, comprising approximately one-third of the total length.

Mode of reproduction. The only information available on this topic is a note by de Witte (1953) on two gravid *Feylinia currori,* which contained two and three "embryons." This meager evidence suggests that *F. currori* is probably live-bearing.

Distribution. Central and west Africa and Principe Island, primarily in lowland, evergreen forest (Fig. 3).

Genera. Two genera and four species are currently recognized in the subfamily Feylininae:

Feylinia Gray, 1845; 3 species; central and west Africa and Principe Island.

Chabanaudia de Witte and Laurent, 1943; 1 species; Gabon.

Discussion. Chabanaudia has been separated from the genus *Feylinia* by de Witte and Laurent (1943) on the basis of its single rather than double postrostral scale. As I have not examined a skull of the single species of *Chabanaudia* (*boulengeri*), I can add nothing to our knowledge of its generic characters or relationships.

Feylinia is, on the basis of osteoderms and the secondary palate, clearly a skink and, according to Miller (1966a), the cochlear duct of *Feylinia* is so "similar in all details to the scincid duct that it may be included in that general group."

Boulenger (1887) distinguished *Feylinia, Typhlosaurus,* and *Anelytropsis* as a separate family (Anelytropidae) and regarded it as a "degraded type of the *Scincidae* (italics his), with which they are closely connected through the genus *Acontias.*" As will be shown below, *Typhlosaurus* is indeed very closely related to *Acontias,* comprising, with this genus and the monotypic *Acontophiops,* a separate subfamily of skinks.

The affinities of the rare monotypic Mexican genus *Anelytropsis* are not so clear, however. Recent studies of the cochlear duct (Miller, 1966b), skull (McDowell, personal communication), and vertebral morphology (Etheridge, 1967) indicate that this genus is perhaps related to the Southeast Asian-New Guinean *Dibamus,* but the broader relationships of these two genera are obscure.

Specimens examined.[1] I have examined the skulls of the following species of feylinines: *Feylinia currori elegans* (MCZ 42886), *F. currori* (MCZ 106990), and *F. polylepis* (MCZ 61215).

Acontinae

Diagnosis. Frontal bone divided (Fig. 1); palatine bones just separated ventrally along midline of secondary palate; palatine in broad contact with ectopterygoid along posterior edge of infraorbital vacuity, thereby usurping extensive contact of pterygoid with ectopterygoid and excluding palatal ramus of pterygoid from a position on infraorbital vacuity (Fig. 2).

Supratemporal arch and post–temporal fenestra usually completely lacking (except in *Acontias plumbeus* and *Typhlosaurus lineatus,* see below). Prefrontal and squamosal bones reduced in size (except in *Acontias plumbeus* and *Typhlosaurus lineatus*), the squamosal especially so, being much smaller than the supratemporal bone directly posterior to it.

Maxilla borders orbit ventrally, the jugal being reduced to a small, vertical element suspended between postfrontal and maxilla.

Four to six teeth on premaxillae and three to ten teeth on maxilla.

Meckel's groove closed and fused.

Rostral and mental scales greatly enlarged, the external naris being situated well forward in rostral and connected to its posterior edge by a horizontal suture. No external trace of limbs. A single, transversely enlarged preanal scale. Tail less than 22 per cent of total length.

Description of skull. Detailed descrip-

[1] Abbreviations used in this section and similar sections to follow will be found on pp. 180 and 181.

tions of the skull of *Acontias meleagris* have been provided by de Villiers (1939), Brock (1941), and van de Merwe (1944), and figures of the skulls of *Acontias plumbeus* and *Typhlosaurus aurantiacus* in Peters (1882). As practically all the important skull features of the subfamily can be seen in the well-described *A. meleagris*, no more than a brief description of the skull morphology characteristic for the group will be given here.

As is generally true in other burrowing lizards, the postorbital region of the skull has become elongated, a feature which, along with the blunt rounded snout, gives the whole skull a bullet-shaped appearance.

The palatines are two long, almost complete scroll-like tubes whose ventral sides approach closely, but do not meet, along the midline of the palate. The medial sides of the palatines do touch, however, and articulate with medial posterior projections of the vomers to separate partially two tubular air passages.

The palatine is in broad contact with the ectopterygoid along the posterior edge of the infraorbital vacuity. The palatal ramus of the pterygoid thus lacks the broad contact with the ectopterygoid seen in all other skinks and is completely excluded from the edge of the infraorbital vacuity. The pterygoids are also widely separated from one another along the midline of the palate (Fig. 2).

The premaxillae, vomers, nasals, and frontals are divided by a median suture. Closely apposed medial processes from the vomers project posteriorly for about half the length of the palatines and articulate with the closely apposed medial sides of the palatines to separate partially the two air passages formed by the scroll-like palatines.

The parietal bone is single; there is a parietal foramen in the anterior part of the parietal, although in some specimens it tends to be covered dorsally with a bony boss.

A long, thin, anteriorly projecting process from each frontal bone wedges part way between the nasal and maxilla to separate the reduced prefrontal from the nasal. The prefrontal is a very small bone on the dorsal edge of the orbit, which articulates with the postfrontal to exclude the frontal from the orbit.

Lateral descending processes from each frontal approach closely or meet below the forebrain. The lateral descending parietal processes are expanded longitudinally to varying degrees, thereby enclosing the hindbrain to varying degrees.

The supratemporal arch and the post-temporal fenestra are lacking, except in *Acontias plumbeus*, which has retained both the arch and the fenestra, and *Typhlosaurus lineatus*, which has retained the supratemporal arch but has lost the post-temporal fenestra. The postfrontal and squamosal are reduced in size, the squamosal especially so, being much smaller than the supratemporal bone directly posterior to it. In *A. plumbeus* and *T. lineatus* the squamosal and postfrontal are well developed and form a supratemporal arch. There is also a clear post-temporal fenestra in *A. plumbeus*, but not in *T. lineatus*. All species in the subfamily lack the post-orbital bone.

The jugal does not take part with the maxilla in forming the ventral border of the orbit as in most skinks, but is reduced to a small vertical element hanging between the postfrontal and maxilla. An epipterygoid is present.

The quadrate is short, stout, and slightly concave posteriorly. The end of the bony shaft of the stapes never articulates directly with the quadrate. In some species (e.g., *Typhlosaurus caecus* and *T. vermis*), however, the quadrate is very compressed, and the shaft of the stapes projects anteriorly, oblique to the lateral edge of the quadrate.

Teeth are present only on the premaxillae, maxillae, and dentaries. The number of teeth ranges from four to six on the premaxillae and from three to ten on

the maxilla. The maxillary teeth vary from the short, blunt crushing teeth of *Acontias plumbeus* to the pointed, slightly curved teeth of *Typhlosaurus vermis.*

The skull and mandible lack pigment.

In the lower jaw, the articular, prearticular, and surangular are usually fused, although the labial suture between the surangular and articular may be evident. The splenial is usually reduced in size, but the angular is well developed. Meckel's groove is obliterated by the overlapping and fusion of the dentary.

Description of external characters. The rostral and mental scales are greatly enlarged. The external naris is situated well forward in the large rostral and is connected with its posterior suture through a horizontal suture. The middorsal head scales consist of one to three single, large, median scales between the posterior edge of the enlarged rostral and a pair of parietals.

The external ear opening is completely covered by scaly epidermis. The body scales are smooth and disposed in 12 to 20 longitudinal rows at midbody. There is a single, transversely enlarged preanal scale.

All external traces of limbs are lacking, although there are rudimentary pectoral and pelvic girdles (Essex, 1928). The tail is very short, comprising less than 22 per cent of the total length.

Mode of reproduction. The three species of acontines for which the mode of reproduction is known (*Acontias meleagris, Typhlosaurus bicolor,* and *T. lineatus*) are live-bearing and produce one to four young in a clutch.

Distribution. Southern Africa with an isolated population in extreme southeastern Kenya (Fig. 3).

Genera. Only three genera, encompassing 15 species, are included in the subfamily:

Acontias Cuvier, 1817; 6 species; southern Africa, with an isolated population in extreme southeastern Kenya.

Acontophiops Sternfeld, 1911; 1 species; northern Transvaal of South Africa.

Typhlosaurus Wiegmann, 1834; 8 species; southern Africa.

Discussion. An important problem is the status of the Malagasy *Acontias.* Boulenger (1887) included Cingalese and Malagasy species as well as South African species in his genus *Acontias.* Hewitt (1929) pointed out certain differences in the head scales and tubular system of the osteoderms among the *Acontias* of Ceylon, Madagascar, and Africa. He thereupon referred the Cingalese skinks to their (original) genus *Nessia* Gray, 1839 (type species: *burtoni*), and proposed the generic name *Pseudacontias* for the two Malagasy species (type species: *holomelas*), leaving the name *Acontias* Cuvier, 1817 (type species: *meleagris*), for the mainland African forms.

M. A. Smith (1935) noticed the great differences in the relationships of the bones of the palate between *Nessia* and *Acontias* (outlined here in the diagnoses of the respective subfamilies, the Scincinae and Acontinae) and supported Hewitt's taxonomic decisions for these two groups.

Angel (1942) noted that the generic name *Pseudacontias* Hewitt, 1929, was preoccupied by *Pseudacontias* Bocage, 1889, another genus of Malagasy skinks, and, minimizing the differences pointed out by Hewitt (1929), put the two disputed Malagasy skinks back in *Acontias.*

In addition to the differences in the tubular pattern of the osteoderms and the relationships of certain head scales, Hewitt (1929) had noted that the *Acontias* of Africa differed from those of Madagascar in having very much shorter tails and fewer scales around midbody. These two differences distinguish the subfamily Acontinae and the subfamily next discussed, the Scincinae, to which in fact the Malagasy (and the Cingalese *Nessia*) belong. The skull differences between South African *Acontias* and Malagasy *Acontias* are also those of the two subfamilies.

I have examined only the secondary

Figure 3. Distribution of the Feylininae and Acontinae, two subfamilies which have apparently evolved independently from the scincines in Africa.

palate in the skull of the Malagasy *Acontias,* and both species differ from *Nessia* (*layardi*) in having the posteromedial edges of the palatal rami of the pterygoids smoothly diverging, instead of deeply emarginated as in *Nessia.* Such palatal differences are indicative of generic separation. I therefore suggest that the two species of Malagasy "*Acontias*" (*holomelas* and *hildebrandti*) be placed in a distinct genus which may be known as

Malacontias[1] new genus

The type species, herewith designated, is *Acontias holomelas* Günther, 1877.

Specimens examined. The skulls of the following acontine species have been examined:

ACONTIAS: breviceps (MCZ 38559), *g. gracilicauda* (MCZ 100905), *g. occidentalis* (MCZ 67859, 67861), *g. tasmani* (MCZ 96905), *lineatus* (MCZ 21416, 21659), *meleagris* (MCZ 11934, FMNH 84189), *plumbeus* (MCZ 14233), *percivali* (MCZ 40180).

TYPHLOSAURUS: caecus (AMNH 50669), *cregoi* (MCZ 41935), *lineatus* (FMNH 142754), *vermis* (MCZ 41938).

Scincinae

Diagnosis. Frontal bone divided (Fig. 1). Palatines almost always separated medially except in some *Scelotes, Proscelotes* and *Gongylomorphus*[2] *bojeri.* Palatal rami of pterygoids almost always separated medially except in *Gongylomorphus bojeri* and the three endemic "*Scelotes*" of the Seychelles (*gardinieri, braueri* and *veseyfitzgeraldi*). Palatine bones widely separated from ectopterygoid along posterior edge of infraorbital vacuity in most genera and species, i.e., palatal ramus of pterygoid borders infraorbital vacuity and articulates with ectopterygoid along posterior edge of this vacuity (Fig. 2). In a few species, ectopterygoid contacts palatine along posterior edge of infraorbital vacuity by anteriorly projecting process that excludes palatal ramus of pterygoid from infraorbital vacuity.

Supratemporal arch complete, i.e., squamosal and postfrontal bones always in contact directly or by way of postorbital bone. Lateral descending processes from parietal to epipterygoid sometimes expanded longitudinally, but more frequently simply fingerlike projections.

Nostril usually pierced in rostral, or between rostral and various other small head scales, or between two or more small head scales, rarely in large, discrete nasal scale. Limbs present in most species. At least one pair of enlarged preanal scales; tail more than 30 per cent of the total length.

Description of skull. The skulls of the following scincines have been figured and discussed in the literature: *Barkudia insularis* (Ganapati and Rajyalakshmi, 1958); *Chalcides guentheri* (Haas, 1936); *Chalcides ocellatus* (Kamel, 1965); *Chalcides* sp. (Romer, 1956); *Eumeces schneideri* (Duméril and Bocourt, 1881); *Eumeces quinquelineatus* (Rice, 1920); *Eumeces* spp. (Kingman, 1932); *Nessia smithi* (Deraniyagala, 1953); *Scincus scincus* (El-Toubi, 1938); *Voeltzkowia mira* (Rabanus, 1911).

The palatine bones are apposed to varying degrees, but do not actually meet along the ventral midline except in some *Scelotes, Proscelotes,* and *Gongylomorphus,* where the palatines meet along their medial edges to various degrees. Dorsally the palatines meet above the air passage.

The pterygoids (palatal rami) are always separated medially except in *Gongylomorphus bojeri* from Mauritius and the three endemic "*Scelotes*" on the Seychelles.

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[1] The generic name *Malacontias* derives from the first syllable of the word "Malagasy"—an inhabitant of Madagascar—and the previous generic name (*Acontias*) for the species now placed in the new genus.

[2] Loveridge (1957) has shown that the generic name *Thyrus* Gray, 1845, for the endemic Mauritian scincine is antedated by the more unwieldy name *Gongylomorphus* Fitzinger, 1843.

In these species the palatines and pterygoids form as complete a secondary palate as that seen in any lygosomine.

The palatine is usually separated from the ectopterygoid by the palatal ramus of the pterygoid along the posterior edge of the infraorbital vacuity, but in the genus *Scincus* and in a few species or even individuals of one species of some genera (e.g., *Chalcides ocellatus* and "*Scelotes*" *astrolabi*), the ectopterygoid may make contact with the palatine by an anteriorly projecting process that excludes the palatal ramus of the pterygoid from the infraorbital vacuity.

At the anterior edge of the infraorbital vacuity, the ectopterygoid may extend along the bordering edge of the maxilla to varying degrees and in some species may actually articulate with the palatines to exclude completely the maxilla from the infraorbital vacuity.

The premaxillae and vomers may be paired, partially fused, or completely fused. The nasals and frontal are always divided. The parietal is single and bears a parietal foramen.

The frontal may form a surface suture with the maxilla to separate the nasal and prefrontal, or the nasal may articulate with the prefrontal to separate the frontal and maxilla, or all four bones may meet at a point.

Lateral descending processes from the frontal may be present or absent. When present, they may be long and deep, virtually meeting below the forebrain. Lateral parietal processes are always present and are usually fingerlike projections to the epipterygoid. In some species, however, the parietal processes become somewhat expanded longitudinally, enclosing part of the hindbrain. This is especially true of species adapted to a burrowing existence.

The post-temporal fenestra is often reduced or obliterated in burrowing species, but otherwise the arch is usually present. The postfrontal and squamosal bones are always present and in contact with one another directly or through a separate postorbital bone. An epipterygoid is always present, as is the jugal in all species examined except in the closely related *Typhlacontias gracilis*, *T. rohani*, and *Fitzsimonsia brevipes*.

The quadrate is usually concave posteriorly and convex anteriorly, although in some species this bone becomes very stout and rodlike. The bony shaft of the stapes articulates directly with the quadrate in some genera (*Fitzsimonsia*, *Melanoseps*, *Ophiomorus*, *Scolecoseps*, *Typhlacontias*, and *Brachymeles vermis*, although in no other species of *Brachymeles* examined). In these scincines, as in the feylinines, the distal end of the stapes abuts against a ventral inflection of a posteriorly projecting nub of the quadrate.

Teeth are always present on the premaxillae, maxillae, and dentaries. In some species teeth also occur on the palatal ramus of the pterygoid. There may be 5–11 teeth on the premaxillae, although many genera are characterized by having fewer than nine premaxillary teeth. The number of teeth on the maxilla varies from 10–25.

The skull may contain some pigment, although usually it does not.

The surangular, articular, and prearticular bones may be distinct or variously fused to one another. The splenial and angular are always distinct except in *Gongylomorphus bojeri*, where the angular is fused to the surangular, articular, and prearticular. Meckel's groove is open in all but a few species.

Description of external characters. The head scales in members of this subfamily are extremely variable. The external naris may be situated entirely in the rostral, between the rostral and one or more of the small head scales (diagnosis of Mittleman's subfamily Chalcidinae), between two or more smaller head scales exclusively, or, less frequently, entirely within a discrete nasal scale (diagnosis of Mittleman's subfamily Scincinae).

An external ear opening may or may not

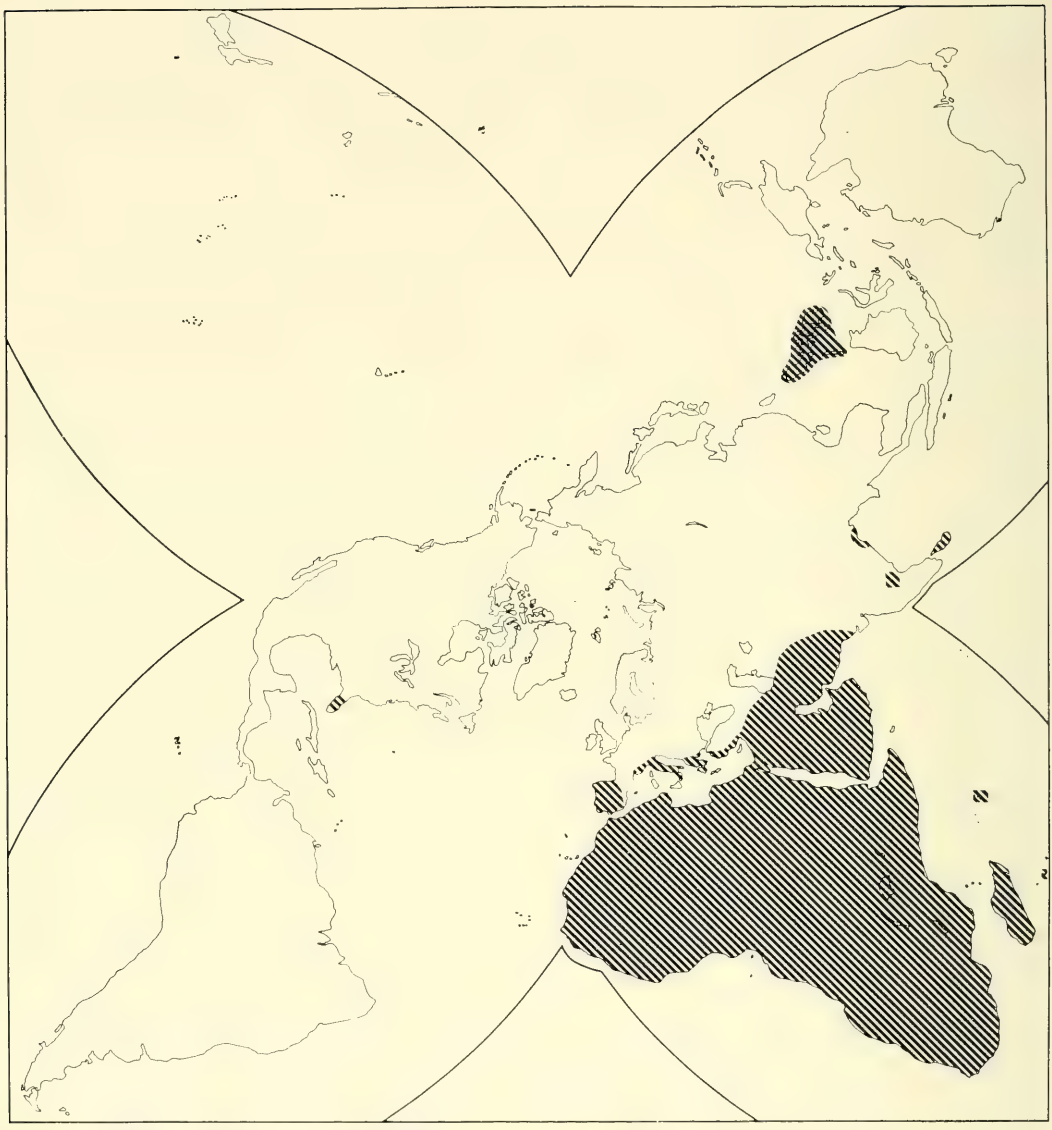

Figure 4. Distribution of the Scincinae (exclusive of the genus *Eumeces*), the most primitive subfamily of skinks.

be present. The body scales are cycloid, imbricate, and generally smooth. The scales are disposed in 14–42 longitudinal rows at midbody, and there are two or more preanal scales.

Limb reduction is a common trend in the subfamily, although only about 28 of the approximately 182 species totally lack any external trace of limbs.

Mode of reproduction. Of the 44 species of scincines for which the mode of reproduction is known, half lay eggs and half bear living young, and, as yet, only in the genus *Eumeces* is the mode of reproduction known to transcend taxonomic boundaries.

Distribution. With the exception of *Eumeces*, the genera of scincines show a disjunct distribution in east and south

central Asia. It is only in southwest Asia, north Africa and more especially in Africa south of the Sahara, Madagascar and the islands of the West Indian Ocean that scincines are widely distributed (Fig. 4) and constitute a significant part of the skink fauna.

Eumeces is the largest and most widespread scincine genus (Fig. 5). The group is distributed along the northern periphery of the world distribution of skinks. The "cold" tolerance implied by this distribution has undoubtedly helped *Eumeces* cross the Bering Land Bridge into the New World and probably accounts for the group's success in the high plateau country of Mexico.

There are no scincines in the Indo-Australian Archipelago or the Australian Region.

Genera. The following genera are included in the Scincinae. I have arranged them in geographic order proceeding west through North America into the Old World.

Eumeces Wiegmann, 1834; approximately 46 species; Bermuda, North and Central America; east and southeast Asia; southwest Asia; North Africa (see Fig. 5).

Neoseps Stejneger, 1910; 1 species; south and central Florida.

Brachymeles Duméril and Bibron, 1839; 13 species; Philippine Islands.

Barkudia Annandale, 1917; 1 species; Calcutta and Chilka Lake Area.

Sepsophis Beddome, 1870; 1 species; central and southern India.

Nessia Gray, 1839; 8 species; Ceylon.

Chalcidoseps Boulenger, 1887; 1 species; Ceylon.

Ophiomorus Duméril and Bibron, 1839; 9 species; Greece through southwest Asia to northwest India.

Chalcides Laurenti, 1768; 14 species; southern Europe, southwest Asia, north Africa, Canary Islands.

Scincus Gronovius, 1763; 12 species; north Africa to southwest Asia.

Scincopus Peters, 1864; 1 species; north Africa from Khartoum, Sudan to Mauritania.

Proscelotes de Witte and Laurent, 1943; 3 species; southeast Africa.

Sepsina Bocage, 1866; 5 species; southern Africa.

Scelotes Fitzinger, 1826; 15 species; southern Africa.

Scolecoseps Loveridge, 1920; 2 species, east central Africa.

Fitzsimonsia de Witte and Laurent, 1943; 1 species; southern Africa.

Typhlacontias Bocage, 1873; 5 species; central and southern Africa.

Melanoseps Boulenger, 1887, 2 species; central east Africa and Cameroon.

Pygomeles Grandidier, 1867; 3 species; Madagascar.

Pseudacontias Bocage, 1889; 1 species; Madagascar.

Paracontias Mocquad, 1894; 2 species; Madagascar.

Cryptoscincus Mocquad, 1906; 1 species; Madagascar.

Grandidierina Mocquad, 1894; 4 species; Madagascar.

Voeltzkowia Boettger, 1893; 1 species; Madagascar.

Malacontias, new generic designation, see p. 162 above; 2 species; Madagascar.

Gongylomorphus Fitzinger, 1843; 1 species; Mauritius.

Incertae sedis, 25 species of Malagasy "*Scelotes*" and 3 endemic "*Scelotes*" of the Seychelles.

Discussion. The systematics of the Malagasy scincines is undoubtedly the biggest problem remaining in the taxonomy of this subfamily. Many species of Malagasy scincines are known from only a few specimens—too few to allow skulls to be prepared. Unfortunately this dearth of specimens is not likely to be remedied in the near future, as many of the species are apparently very secretive in their habits, and Madagascar is not, at present, a popular place for collecting reptiles.

Figure 5. Distribution of the scincine genus *Eumeces*.

The disjunct distribution of the scincine genera in east and central Asia implies, of course, that the scincine ancestors (possibly, but not necessarily, *Eumeces*) were more widespread at one time in the past. Just how widespread these scincines may have been is a very interesting question that future paleontological discoveries may answer. It would be interesting to know, for example, whether the scincines ever inhabited the Australian Region—a region where now only lygosomines are found.

Specimens examined. I have seen the following scincine skulls:

BARKUDIA: insularis (MCZ 54712).

BRACHYMELES: bonitae (MCZ 20129), *gracilis boulengeri* (MCZ field tag 710, MCZ 20131, 26540, 26545, 54253, 26552,

26553, + 1 untagged specimen), *gracilis taylori* (AMNH 86661), *vermis* (MCZ 26587).

CHALCIDES: bedriagai (MCZ 15692), *mionecton* (MCZ 7753, 25145), *ocellatus* (MCZ 9817, 9828, 9837, 9839, 9842, 9844, 9849, 9851, UMMZ 1930, CAS(SU) 18137), *sepsoides* (MCZ 27483, 18351, CAS(SU) 18143).

EUMECES: algeriensis (MCZ 4281), *anthracinus* (MCZ 29312), *brevilineatus* (MCZ 79776), *brevirostris* (FMNH 111614), *chinensis* (MCZ 29005), *copei* (UINHM 33238), *elegans* (MCZ 28983, 28992, 29000), *fasciatus* (MCZ 54126, UINHM 33239, 33240), *gilberti* (USNM 5310), *indubitus* (FMNH 114201), *inexpectatus* (MCZ 45498, 55506), *kishinouyei* (MCZ 55935), *laticeps* (MCZ 55505, + 1 untagged specimen), *latiscutatus* (FMNH 55511), *longirostris* (MCZ 20503, 20508), *lynxe* (MCZ 19086, 19087, 24533, 24534), *marginatus* (MCZ 57111, 57112 part, 7409), *multivirgatus* (UINHM 33244), *obsoletus* (MCZ 35547, 61366, 61367), *ochoterena* (FMNH 114493), *schneideri* (MCZ 6986, UMMZ 2119, 2148), *schwartzei* (USNM 113603), *skiltonianus* (MCZ 6617—2 specimens, 8887, + 1 untagged specimen, CAS 28138), *stimsoni* (CAS 21660), *taeniolatus* (FMNH 1868), *tunganus* (USNM 82751).

FITZSIMONSIA: brevipes (MCZ 96702).

GONGYLOMORPHUS: bojeri (MCZ 46677).

GRANDIDIERINA: lineata (PM 3378).

MALACONTIAS (palatal characters only): *hildebrandti* (PM 99–376), *holomelas* (PM 95–215, 7792).

MELANOSEPS: ater (MCZ 50955, 52487), *occidentalis* (BM 1907.5.22.6A).

NEOSEPS: reynoldsi (MCZ untagged specimen).

NESSIA: layardi (MCZ 38174).

OPHIOMORUS: brevipes (FMNH 141550), *persicus* (FMNH 141557), *raithmai* (AMNH 85846), *tridactylus* (AMNH 75610).

PROSCELOTES: aenea (MCZ 18709), *arnoldi* (MCZ 55145), *eggeli* (MCZ 24217, 24218, 24220).

PYGOMELES: braconnieri (PM 1715).

SCELOTES: anguina (MCZ 96791), *arenicolor* (MCZ 14205), *bidigittata* (MCZ 96789), *bipes* (BM XVII.2.F), *brevipes* (MCZ 21237), *caffer* (MCZ 96792), *gronovi* (BM 97.5.15.8), *limpopoensis* (MCZ 96906), *mira* (MCZ 96790), *uluguruensis* (MCZ 24206).

SCINCUS: scincus (MCZ 27456—2 specimens, 27462, 27464).

SCOLECOSEPS: boulengeri (MCZ 18357).

SEPSINA: angolensis (AMNH 40734, FMNH 142793), *bayoni* (BM RR 1967.80), *tetradactylus* (MCZ 42885, 47770—3 specimens, 47775, 56963, 56965, 56967, 85536).

TYPHLACONTIAS: gracilis (USNM 159338), *rohani* (FMNH 142787).

VOELTZKOWIA: mira (MCZ untagged specimen).

Incertae sedis: Malagasy "*Scelotes*": *astrolabi* (MCZ 20953, 20955), *melanura* (MCZ 11733); *splendidus* (FMNH 72086); Seychelles "*Scelotes*": *braueri* (BM 1910.3.18.33), *gardineri* (BM 1910.3.18.91).

Lygosominae

Diagnosis. Frontal bone single (Fig. 1). Palatines usually in contact along ventral midline except in most *Egernia* and *Corucia zebrata.* Palatine making contact with ectopterygoid if at all only through an anteriorly projecting ectopterygoid process; palatal ramus of pterygoid but not palatine itself in broad contact with ectopterygoid along posterior edge of infraorbital vacuity (Fig. 2). Supratemporal arch complete, i.e., postfrontal and squamosal always in contact directly or by way of postorbital bone; post-temporal fenestra obliterated in some species. Lateral descending processes from frontal not large when present; lateral descending processes from parietal only fingerlike projections to epipterygoid.

Single discrete nasal scale (except in *Sphenomorphus schultzei* and *Ateucho-*

saurus) bearing the external naris; almost always some external indication of limbs (limbs totally lacking in only four of 600+ species in the subfamily); at least one pair of preanal scales; tail more than 30 per cent (usually 50 per cent or more) of total length.

Description of skull. A number of descriptions of the skulls of single species in this subfamily have been published as follows: *Ablepharus pannonicus* (Haas, 1935); *Didosaurus mauritianus* (Hoffstetter, 1945 and 1949); *Lygosoma* sp. (Pearson, 1921); *Mabuya carinata* (Rao and Ramaswami, 1952); *Sphenomorphus quoyi* (King, 1964). In addition, there are figures of whole skulls of *Dasia smaragdina*, *Ctenotus leseuri*, *Mabuya multifasciata*, *Sphenomorphus australe*, and *S. quoyi* in Siebenrock (1892), and Brühl (1886) figures the skull of *Tiliqua rugosa*. Waite (1929) figures ventral palatal views of *Sphenomorphus quoyi*, *Egernia stokesi*, and *Tiliqua* sp. and Duméril and Bocourt (1881) figure a ventral view of the skull of *Mabuya mabouya*. Mitchell (1950) also has line drawings of the palates of several *Egernia* and *Tiliqua*, and Greer (1967a and b) and Greer and Parker (1968) figure the palates of *"Ablepharus" lineoocellatus*, *"Ablepharus" smithi*, *Carlia bicarinata*, *Emoia samoense*, *Eumecia anchietae*, *Geomyersia glabra*, *"Leiolopisma" metallica*, *Leptosiaphos blochmanni*, *Lerista elegans*, *L. bougainvilli*, *Mabuya polytropis*, *Riopa punctata*, and *Sphenomorphus pardalis*.

The general shape of the skull is highly variable. In burrowing forms the postorbital region may be elongate and the whole skull bullet-shaped, or conversely, in surface forms, the skull may be short and rather deep. In other instances the skull may be depressed.

The palatines meet along the ventral midline to form a secondary palate, above which is the main air passage. Anteriorly the palatines arch over this passageway, but posteriorly most of the air passage is enclosed dorsally by a membranous tissue. This is in contrast to the condition in the Acontinae, where the entire dorsal arch of the air canal is formed by the palatine bones.

In only a few species (most *Egernia* and *Corucia zebrata*) are the palatines separated ventrally along the midline. In these species the palatines are never separated by as great a distance as in most of the genera of the more primitive scincines (e.g., *Scincus*, *Eumeces*, and *Chalcides*).

The palatine may or may not be in contact with the ectopterygoid. When the palatine is in contact with the ectopterygoid, it is by means of an anteriorly projecting process from the ectopterygoid. The palatal ramus of the pterygoid is the only bone in broad contact with the ectopterygoid along the posterior edge of the infraorbital vacuity (Fig. 2).

The pterygoids may be in contact along the medial edge of their palatal rami or separated either by the interpterygoid vacuity or by two medioposterior processes of the palatines.

The premaxillae and nasals are paired. The vomer may be single or divided. The frontal and parietal are single. There is a parietal foramen in the anterior part of the parietal except in *Ateuchosaurus*, where the parietal foramen is in the posterior part of the frontal or in a small, median azygous bone between the frontal and parietal.

The frontal may form a surface suture with the maxilla and thereby separate the prefrontal from the nasal, or all four bones may meet at a common point, or the nasal and prefrontal may meet to separate the frontal and maxilla.

There is a pair of descending lateral processes from the frontal in a few species, but these processes are never very deep. There is also a pair of usually well-developed, fingerlike lateral processes descending from the parietal to the ectopterygoid. In some species, however, these parietal processes are barely distinguish-

able from the shallow crest from which they arise.

The post-temporal fenestra is obliterated in burrowing species, but in other forms the fenestra is usually well developed. The primary elements of the supratemporal arch, i.e., the postfrontal and squamosal, are always present and in contact with each other directly or by the intermediary of a postorbital when this bone is present. A well-developed jugal and epipterygoid are always present.

The quadrate tends to become reduced to a short, rodlike element in forms lacking an external ear opening; this modification of the quadrate occurs in non-burrowing species as well as burrowing forms.

Teeth are always present on the premaxillae, maxillae, and dentaries, and are found on the palatal rami of the pterygoids in a few species of several genera. The number of teeth on the premaxillae ranges from 6–15 (usually 9–11) and from 8–40 on the maxilla.

The skull and mandible may or may not contain pigment.

In the mandible the dentary, coronoid, splenial, and angular are always distinct, but the articular, prearticular, and surangular may be fused to various degrees. Meckel's groove may be present or absent or in various states of closure.

Description of external characters. The external naris is in a discrete nasal, although in *Sphenomorphus schultzei* and *Ateuchosaurus* the nasal is fused to the first supralabial. The dorsal head scales most commonly consist of the following scales from anterior to posterior: a single rostral; a single frontonasal; paired supranasals (present or absent); paired prefrontals (fused, meeting along the midline, separated or absent); a single frontal in contact with one to seven of the one to nine supraoculars; paired (or fused) frontoparietals and a single (or fused to the frontoparietals) interparietal, and paired (rarely fused) parietals. The parietal foramen is in the interparietal scale.

An external ear opening may or may not be present. Some species have auricular lobes along the edge of the external ear opening. The body scales are cycloid and imbricate (except in *Tribolonotus*, which has granular and tubercle-like scales on the dorsum and sides) and are either smooth or keeled. At midbody the scales are disposed in 18–112 rows. There are two or more preanals, except in a few species of *Tropidophorus* which have but a single, large preanal scale.

Most of the species have both fore and hind limbs, although digit and limb reduction is a recurrent trend in the group. The fore limbs and digits are usually reduced and lost ahead of the hind limbs and digits. However, in only four of the 600+ species of the subfamily are limbs totally lacking.

Mode of reproduction. The mode of reproduction is known for 193 species of lygosomines; of these 193 species, 124 (64.3 per cent) lay eggs and the remaining 69 (35.7 per cent) are live-bearing.

Distribution. The lygosomines, being the most numerous, in terms of numbers of species, and most diverse subfamily of skinks, are, not surprisingly, the most widespread subfamily (Fig. 6). Lygosomines are best represented both in numbers of species and in diversity of adaptations in the Australian Region. It is also this group, exclusively, that has seeded the far-flung islands of the Pacific, where they extend as far north as the Bonin Islands and Laysan (*Ablepharus boutoni*) and as far south as Stewart Island (*Leiolopisma lineoocellata* and *L. zelandica*).

The lygosomines seem to be absent from the more arid regions of central north Africa and the Arabian Peninsula.

Genera. The genera in this subfamily are as yet too poorly known taxonomically to list. While I do not agree with many of Mittleman's (1952) new generic groupings of lygosomines, his work does provide a convenient list of most of the species in the subfamily. In addition, he provides a

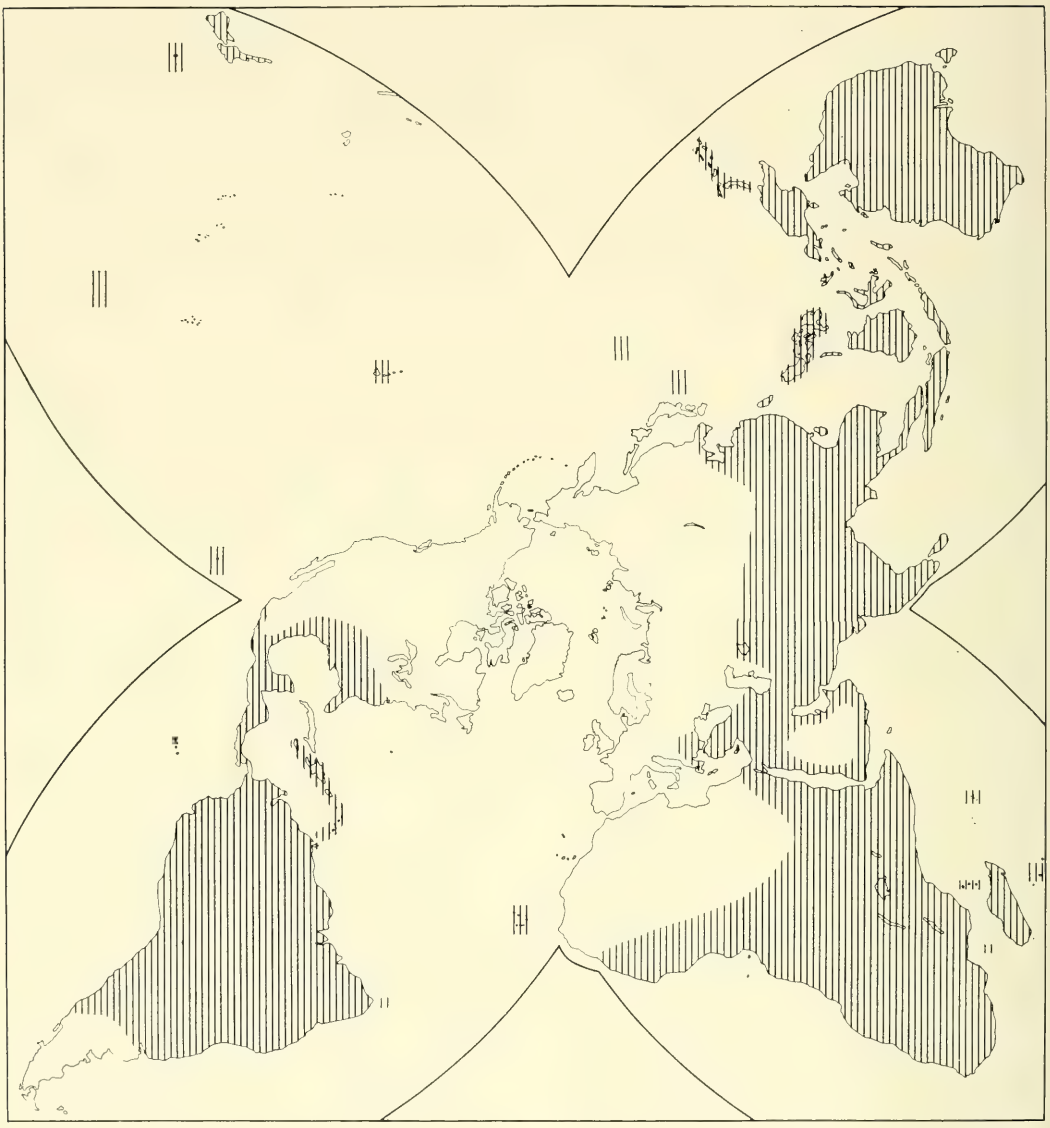

Figure 6. Distribution of the Lygosominae, the most advanced subfamily of skinks. In the oceans only the islands that bound the northern and southern limits of the range are marked with distribution lines.

nearly complete primary generic synonymy.

Mittleman (1952) did not regard the genera *Tiliqua*, *Egernia*, *Corucia*, and *Mabuya* as lygosomines. *Mabuya* and *Tiliqua* fit the diagnosis of the lygosomines as given here in every regard, but some *Egernia* and *Corucia zebrata* differ from other lygosomines in having the palatine bones slightly separated along the midline of the secondary palate. The two genera represented by these species are very closely related (Greer, unpublished work) and on all other characters, especially the fusion of the frontals, are lygosomines.

At this point, the separation of the palatines seems most readily interpreted as

either a secondary separation or, less probably in my mind, as a primitive character retained from a scincine ancestry.

Discussion. The greatest single taxonomic problem with the Lygosominae is the delimitation and relationships of genera. Recent work has shown that among the lygosomines, as well as in other major skink taxa, the correlation of skull and external morphology is a very effective method for recognizing taxa worthy of generic rank (Greer, 1967a and b, and Greer and Parker, 1968).

Specimens examined. Listed below are the skulls of the lygosomine skinks I have examined. In this list I have tried to indicate my present opinions of species' relationships by an informal nomenclature, e.g., alpha and beta *Leiolopisma,* and geography. Some of these groups have been discussed in other papers (Greer and Parker, 1967 and 1968).

ABLEPHARUS: alpha Asian: *brandti* (MCZ 56533), *deserti* (MCZ 5364), *grayanus* (MCZ 84084, CAS 99883), *kitaibeli* (CAS 47453), *pannonicus* (MCZ 3961); alpha Australian: *boutoni* (MCZ 31040), *lineoocellatus* (MCZ 33143, 33144, CAS 77404, BM XL.4.A), *spenceri* (AMNH 83929), *taeniopleurus* (MCZ 35321); beta African: *megalurus* (MCZ 31065), *smithi* (MCZ 42880), *wahlbergi* (MCZ 55827).

ANOTIS: mariae (MCZ 92393).

ATEUCHOSAURUS: pellopleurus (MCZ 55925, 55927), *sowerbyi* (AMNH 34153).

CARLIA: bicarinata (MCZ 64315), *fusca* (MCZ 49412, 49423, 73791, 73793, CAS 100777), *novaeguineae* (MCZ 83758), *vivax* (AMNH 82758).

COPHOSCINCOPUS: durus (MCZ untagged specimen).

CORUCIA: zebrata (MCZ 68815, 72918, 77375, AMNH 69434).

CTENOTUS: australis (MCZ 79537, CAS 76722), *fasciolatus intermedius* (MCZ 35442), *labillardieri* (MCZ 24730), *leonhardi* (MCZ untagged specimen), *leseuri* (MCZ 74891); *spaldingi* (MCZ 35374), *taeniolatus* (MCZ 6302).

DASIA: olivacea (MCZ ex 7726), *semicincta* (MCZ 26414), *smaragdina* (MCZ 4094—2 specimens), *smaragdina moluccarum* (MCZ 7709), *s. perviridis* (MCZ 49315, 72275, 72508), *s. philippinicum* (MCZ 26429), *vittata* (MCZ 16352).

EGERNIA: bungana (FMNH 35146), *cunninghami* (FMNH 31041), *depressa* (MCZ 33062), *formosa* (MCZ 33067, 33070, 33071, 33078, 33076), *hosmeri* (AMNH 87779), *inornata* (MCZ 35289, 35291, 35294, 35297), *kingi* (MCZ 33087), *luctuosa* (MCZ 33104), *m. major* (AMNH 69434), *nitida* (CAS 76619), *stokesi* (MCZ 33105, 33106, 33108, FMNH 51707), *s. striolata* (MCZ 24552), *whiti napoleonis* (MCZ 24491).

EMOIA: adspersa (AMNH 29227), *atrocostata* (MCZ 15074, 15080, 26476, 26479), *boettgeri* (MCZ 22074), *callisticta werneri* (MCZ 67203, 67308, + 3 untagged specimens), *cyanogaster* (MCZ 15121, 15135, 72278, 72287), *cyanura* (MCZ 14582, 14584, 14586, 75954, 75956), *flavigularis* (MCZ 65869), *kordoana* (MCZ 48603), *kuekenthali* (FMNH 134594), *loveridgei* (MCZ 49321), *maculata* (MCZ untagged specimen), *mivarti fuscolineata* (MCZ 73807, 75984), *nigra* (MCZ 15153, 15157, 67770, 72510, 72514, 72515, 72517, 72523, 75522), *p. pallidiceps* (MCZ 79856), *p. physicae* (AMNH 95772), *ruficauda* (MCZ 26482—2 specimens, 26492), *samoensis* (MCZ 16931), *sanfordi* (AMNH 40169), *sorex* (MCZ 7705), *submetallica* (AMNH 59015).

EUGONGYLUS: albofasciolatus (MCZ 4097, 72703), *rufescens* (MCZ 49341).

EUMECIA: anchietae (MCZ 41557, 41562).

GEOMYERSIA: glabra (MCZ 87611).

HEMIERGIS: decresiensis (MCZ 49173), *initiale* (MCZ 74976), *peroni* (MCZ 24648, 24652), *quadrilineatum* (MCZ 33210), *tridactylum* (MCZ 24595).

LEIOLOPISMA: telfairi (MCZ 3077); alpha Asian: *bilineata* (MCZ 3923), *himalayana* (MCZ untagged specimen), *modesta* (AMNH 23669), *reevesi* (MCZ 39234, 39237, 39236); alpha Southeast

Asian-New Guinea: *cheesmanae* (AMNH 62461), *longiceps* (MCZ 48585), *miotis* (MCZ untagged specimen), *noctua* (MCZ 76006, 76008), *pulchella* (MCZ 26440, + 1 untagged specimen), *quadrivittata infralineolata* (MCZ untagged specimen), *q. quadrivittata* (AMNH 86665), *rabori* (AMNH 93698), *semperi* (MCZ 20120); alpha Australian South Pacific: *austrocaledonica* (MCZ 15970), *elegantoides* (MCZ 80111), *entrecasteauxi* (MCZ 33223), *maccoyi* (MCZ 33199), *metallica* (MCZ 67129), *moco* (MCZ untagged specimen), *nigrofasciolata* (MCZ 27943), *pretiosa* (MCZ 10232), *stanleyana* (MCZ 47904, 47906), *suteri* (MCZ untagged specimen), *zelandica* (MCZ 92261); alpha North American: *laterale* (MCZ 2436, CAS 31123), *cherrei cherrei* (MCZ 29400), *c. lampropholis* (MCZ 15479); *flavipes* species group: *flavipes* (MCZ 22189, x-21440), *prehensicauda* (MCZ 85561 + 1 untagged specimen), *virens* (MCZ 76270, 76917, 76920); beta African: *reichenovei* (AMNH 11195); beta Australian: *challengeri* (MCZ 35455, AMNH 82792), *guichenoti* (MCZ 61379), *mustelina* (MCZ 61386), *weeksae* (MCZ 49190).

LEPTOSIAPHOS: blochmanni (MCZ untaggd specimen), *graueri* (MCZ 47662), *kilimense* (MCZ 24189, 41577), *meleagris* (MCZ 47676).

LERISTA: bipes (AMNH 86089), *bougainvillei* (MCZ 61403), *elegans* (FMNH 11319), *fragilis* (MCZ 42988, CAS 77190), *gerrardi* (MCZ 33255), *lineata* (MCZ 33265), *lineopunctulata* (BM 1902.7.30.5), *miopa* (MCZ 33260), *muelleri* (MCZ 86699), *planiventrale* (BM 1954.1–2.21), *praepedita* (MCZ 33265), *punctatovittata* (MCZ 79494), *tetradactyla* (BM 1902.7.30 .6), *timida* (MCZ 13246).

LYGOSOMA: equale (MCZ 35344), *quadrupes* (MCZ 20518), *verreauxi* (MCZ 10263).

MABUYA: aurata septentaeniata (MCZ 56550), *bayoni* (MCZ 39731), *bensoni* (MCZ 22583), *binotata* (MCZ 22421), *blandingi* (MCZ 55171), *brachypoda* (MCZ 71410), *brevicollis* (MCZ 41306), *capensis* (MCZ 21433), *comorensis* (MCZ 24151—2 specimens, 24155), *dorsovittata* (MCZ untagged specimen), *elegans* (MCZ 67954), *englei* (MCZ untagged specimen), *fasciata* (MCZ 37835 + 2 untagged specimens), *f. frenata* (MCZ 49547), *gravenhorsti* (MCZ 11609), *hildebrandti* (MCZ 70248, 70254), *lacertiformis* (MCZ untagged specimen), *mabouya* (CAS 71456, UMMZ s-1047), *m. mabouya* (MCZ 32040, 38935, 54201, 81182, 81184), *m. sloani* (MCZ 36617), *macrorhyncha* (MCZ 49551, 49552), *macularia* (MCZ untagged specimen), *maculilabris* (MCZ 24820, 24821), *megalura* (MCZ 47611), *multicarinata* (CAS 60430), *multifasciata* (MCZ 25198, 25199, 37843, CAS 60692, 362 + 2 untagged specimens, UMMZ s-1831, s-1830), *occidentalis* (MCZ 43180), *perroteti* (MCZ 19711), *planifrons* (MCZ 54559, 85545), *polytropis* (MCZ 8103), *quinquetaeniata margaritifer* (MCZ 52424—2 specimens, 55179, 67838–67840), *sulcata* (MCZ 21645), *striata* (MCZ 74472–74474), *varia* (MCZ 18658—2 specimens, 18668, 50823, 50824, 85543).

MENETIA: greyi (MCZ 79498).

OPHIOSCINCUS: anguinoides (MCZ 74098), *roulei* (MCZ 74099).

PANAPSIS: breviceps (MCZ untagged specimen).

RIOPA: afer (MCZ 41517, 41519, 71881), *albopunctata* (MCZ 8360, UMMZ 122269), *bowringi* (MCZ untagged specimen, CAS 60737), *fernandi* (MCZ 49696), *laeviceps* (MCZ 71889), *lineata* (AMNH 46379), *mabuiiformis* (MCZ 40267), *pembana* (MCZ 46106), *popae* (MCZ 44706), *punctata* (MCZ 3238), *sundevalli* (MCZ 41537, 41543), *tanae* (MCZ untagged specimen), *vinciguerrae* (MCZ 17892).

RISTELLA: beddomi (BM 82.5.22.152), *guentheri* (BM 82.5.22.137), *rurki* (BM 74.4.29.1329), *travancorica* (BM 74.4.29 .437).

SPHENOMORPHUS: fasciatus species group: *antimorus* (MCZ 25374), *australe*

(MCZ 24568), *cranei* (MCZ 76048), *crassicaudus* (MCZ untagged specimen, AMNH 82606), *elegantulus* (BM 83.4.14.20), *emigrans* (MCZ 27043), *fasciatus* (MCZ 26357), *maindroni* (MCZ 64273, 72737), *muelleri* (MCZ untagged specimen), *nigricaudus* (MCZ 35407), *p. pardalis* (MCZ 35413), *pratti* (MCZ 48596), *pumilus* (MCZ 48824), *punctulatus* (MCZ 5250), *quoyi* (MCZ 3301, 3307, 79549, 79552), *rufus* (MCZ 47064), *solomonis* (MCZ 72618, 72626, 72664, 72665, 77373, 77374), *tanneri* (MCZ 76507, 76509, 89126, 92227), *tenuis* (MCZ 35398), *tryoni* (MCZ 35387, 35388); *variegatus* species group: *acutus* (MCZ 20114), *aignanus* (BM 1946.8.15.48), *anomalopus* (MCZ 37849), *boulengeri* (AMNH 33180), *concinnatus* (MCZ 72732, 72733, 91426), *cumingi* (MCZ 20113), *darlingtoni* (MCZ 83965), *dussumieri* (BM 1946.8.15.42), *florensis nitidus* (MCZ 27018, 27019, 27022, 27024), *formosensis* (AMNH 34909), *fragosus* (MCZ 92267), *granulatus* (AMNH 95782), *i. indicus* (MCZ 44724), *j. jobiensis* (MCZ 44190, 99336, BM 1935.5 .10.108), *maculatus* (MCZ 3336), *melanopogon* (MCZ 68919, x-10113), *nigrolabris* (FMNH 14255, BM 96.4.29.19–21), *sanctus* (MCZ 7663), *striolatus* (MCZ 27034), *taylori* (MCZ 78090), *tersus* (MCZ 39284), *variegatus* (MCZ 25398); alpha *SPHENOMORPHUS: bignelli* (MCZ 19602), *minutus* (MCZ 54259), *ornatus* (MCZ 6154); *incertae sedis: fallax* (MCZ 19602), *louisiadense* (BM 1946.8.19.25), *monotropis* (BM 1908.5.28.54–55), *striatopunctatus* (BM 1948.1.7.60).

TILIQUA: branchiale (MCZ 78652), *nigrolutea* (MCZ 1077—2 specimens, FMNH 22498), *occipitalis multifasciata* (MCZ 35310), *rugosus* (MCZ 24456, UMMZ s-2346), *scincoides* (MCZ 65221, UMMZ s-1864, s-1863, FMNH 51702, 51710).

TROPIDOPHORUS: beccari (MCZ 43524), *laotus* (MCZ 100512), *misaminus* (MCZ 44163—3 specimens), *robinsoni* (MCZ 39374).

TRIBOLONOTUS: blanchardi (MCZ 72763), *gracilis* (AMNH 82364), *novaeguineae* (MCZ 21063), *pseudoponceleti* (MCZ 72766, 76424, 76425, 76456), *schmidti* (AMNH 66219).

A KEY TO THE SUBFAMILIES OF SKINKS

The following key is as much a review of the diagnostic characters of the subfamilies of skinks as it is a device for their identification. In each section the character states are listed in the order of their taxonomic importance.

1. Frontal bones separate (Fig. 1); palatine bones separated ventrally along midline of secondary palate (Fig. 2), except in some *Scelotes, Proscelotes,* and *Gongylomorphus bojeri;* supratemporal arch complete or incomplete; external naris often not in a discrete nasal scale; many species without any trace of limbs 2

Frontal bones fused (Fig. 1); palatine bones meeting ventrally along midline of secondary palate (Fig. 2), except in some *Egernia* and *Corucia zebrata;* supratemporal arch always complete; external naris almost always in a discrete nasal scale; rarely without any external trace of limbs ..... LYGOSOMINAE

2. Palatine excluded from position on infraorbital vacuity by anteriorly projecting process from palatal ramus of pterygoid to maxilla (Fig. 2); nasal bones fused; jugal absent; supratemporal arch complete ..... FEYLININAE

Palatine borders edge of infraorbital vacuity (Fig. 2); nasal bones separate; jugal present except in *Typhlacontias gracilis, T. rohani,* and *Fitzsimonsia brevipes;* supratemporal arch complete or incomplete 3

3. Palatines in broad contact with ectopterygoid along posterior edge of infraorbital vacuity to partial exclusion of palatal ramus of pterygoid (Fig. 1); supratemporal arch incomplete except in *Acontias plumbeus* and *Typhlosaurus lineatus;* 4–6 teeth on premaxillae, 3–10 teeth on maxilla; limbless; a single transversely en-

larged preanal scale; tail 22 per cent or less of total length ..... ACONTINAE

Palatines separated from ectopterygoid by palatal ramus of pterygoid along posterior edge of infraorbital vacuity (Fig. 2) or palatines in contact with ectopterygoid by way of anteriorly projecting process from ectopterygoid that excludes palatal ramus of pterygoid from a position on infraorbital vacuity, but palatine never excludes the palatal ramus of pterygoid from a major contact with ectopterygoid as in Acontinae; supratemporal arch complete; 5–11 teeth on premaxillae, 10–25 teeth on maxilla; only a few species lack any trace of limbs; at least two preanal scales; tail 30 per cent or more of total length ..... SCINCINAE

FOSSIL RECORD OF SKINKS

In spite of the great diversity and abundance of skinks today, the family has a very poor fossil record (Hoffstetter, 1944 and 1961). Only two genera of pre-Pleistocene fossil skinks have been accurately reported.

Sauriscus cooki (Estes, 1964a) is known from the late Cretaceous Lance Formation of eastern Wyoming. The diagnostic characters of the available fragments, i.e., weakly bifid teeth and striations on the lingual surface of the tooth crown, do not serve to align the species with any living skink. If the fossil is in fact a skink, rather than a representative of another scincomorph family, its primary importance is that it indicates that skinks were extant by at least the late Cretaceous.

All other skink fossils are referable to the scincine genus *Eumeces* and come from deposits within the present geographic range of the genus. The oldest of these fossils is Oligocene in age (Estes, 1964b) and is as easily recognizable as a *Eumeces* as is any recent skull. The later, pre-Pleistocene fossils of *Eumeces* are distributed as follows: early Miocene of Florida (Estes, 1963), Miocene of Morocco (Hoffstetter, 1961), Mio-Pliocene of Nebraska (Estes and Tihen, 1964), and the late Pliocene of Kansas (Taylor, 1941, and Twente, 1952).

PHYLOGENY OF THE FOUR SUBFAMILIES OF SKINKS

Although the fossil record is thus of little value in elucidating the phylogeny of skinks, much can be inferred from the morphology and distribution of living species. The strength of this approach to the phylogeny of skinks, or any other group without a fossil record, for that matter, is, of course, only as sound as the reasons given for believing that one particular character state is historically antecedent to other alternative and contemporaneous character states. For the present, I will limit the discussion to the four subfamilies of skinks. The phylogenetic relationships of lower level taxa will be considered separately in papers on those taxa.

The fusion and loss of bones in the skull, the reduction and loss of appendages, and the acquisition of live-bearing habits are general trends in vertebrate evolution and are accepted here as advanced character states for skinks. Thus the fusion of the nasals and frontals,[1] the loss of the jugal and postorbital bones, and an incomplete supratemporal arch are advanced characters, as are complete limblessness and a live-bearing mode of reproduction.

Other clear evolutionary trends among

[1] That paired frontals are antecedent to the single frontal in skinks is supported by evidence from the ontogenetic development of this bone in lygosomine skinks. In the embryos of the live-bearing lygosomines I have examined (*Eumecia anchietae, Hemiergis tridactylus, Leiolopisma elegantoides lobula, Mabuya lacertiformis, Sphenomorphus australe,* S. *concinnatus,* and S. *quoyi;* also *Lygosoma* sp. according to Pearson, 1921), there are two centers of ossification in the development of the single frontal of the adult. The frontals remain separated in these embryos until quite late in development (squamation and color pattern fully developed) but have fused by the time of hatching.

squamates, such as the loss of pterygoid teeth and the loss of an external ear opening, also help in reconstructing the phylogeny of skinks (Fig. 7).

The formation of the bony secondary palate in the four subfamilies of skinks offers further clues to phylogeny. First, it should be pointed out that with the exception of *Anelytropsis* and *Dibamus*, the bony secondary palate of skinks is unique among squamates and has surely been derived from the primary palate of other lizards.

The secondary palates of the Feylininae and Acontinae are quite different from one another, and both palatal types are also quite complex, suggesting that they have been derived independently from some less complex palate.

Of the two remaining subfamilies of skinks, the scincine secondary palate appears to be more primitive than and ancestral to the lygosomine palate. The basic differences between the palates of the two taxa are that, in general (the exceptions will be discussed below), the scincines have the palatine bones apposed but not meeting on the midline, and the palatal rami of the pterygoids are widely separated, whereas the lygosomines have at least the palatines meeting medially, and in some groups the palatal rami of the pterygoids meet as well. Three lines of evidence indicate that the sequence of palatines and pterygoids not meeting medially (general scincine condition), palatines but not pterygoids meeting medially, and palatines and pterygoids both meeting medially (the two general lygosomine conditions) is in fact probably the actual developmental sequence in the evolution of a complete secondary palate in skinks.

(1) To derive the complete secondary palate of scincids from the non-scincid squamate primary palate, one would expect *a priori* that a proto condition to the medial contact of the palatines and pterygoids of the complete secondary palate would be the progressively closer medial apposition of these bones, instead of the construction of a complete secondary palate in one macromutation. It would also be functionally more efficient first to appose the more anterior bones of the primary palate (the palatines) before the more posterior bones (the pterygoids) were incorporated; that is, it is difficult to imagine the efficiency of a secondary palate consisting of the pterygoids in contact medially but the palatines widely separated.

(2) The development of a secondary palate in different groups in the fossil record, e.g., turtles and crocodilians, involves the progressive incorporation of successively posterior bones of the primary palate.

(3) The ontogenetic development of a complete secondary palate in lygosomines involves first the medial closure of the palatines, followed by the closure of the palatal rami of the pterygoids.

The close correlation between the closure of the palatines on the midline of the secondary palate and the fusion of the frontals is the primary justification for recognizing the lygosomines as a distinct taxon of skinks. And in that the divided frontals and the separated palatine bones in the secondary palate of the scincines are primitive characters, the lygosomines must be considered an advanced group derivable from the scincines. Those few lygosomines which have the palatines not quite meeting along the midline of the palate and those few scincines which do have the palatines and sometimes the pterygoids meeting along the midline of the palate do no damage to the foregoing outline of the phylogeny of the scincines and lygosomines.

Thus the lygosomines in which the palatines do not quite meet medially (most *Egernia* and *Corucia zebrata*) may be either very primitive lygosomines, in which the palatines have never met medially, or they may be advanced lygosomines, in which the palatines are secondarily separated. Although the two genera to which

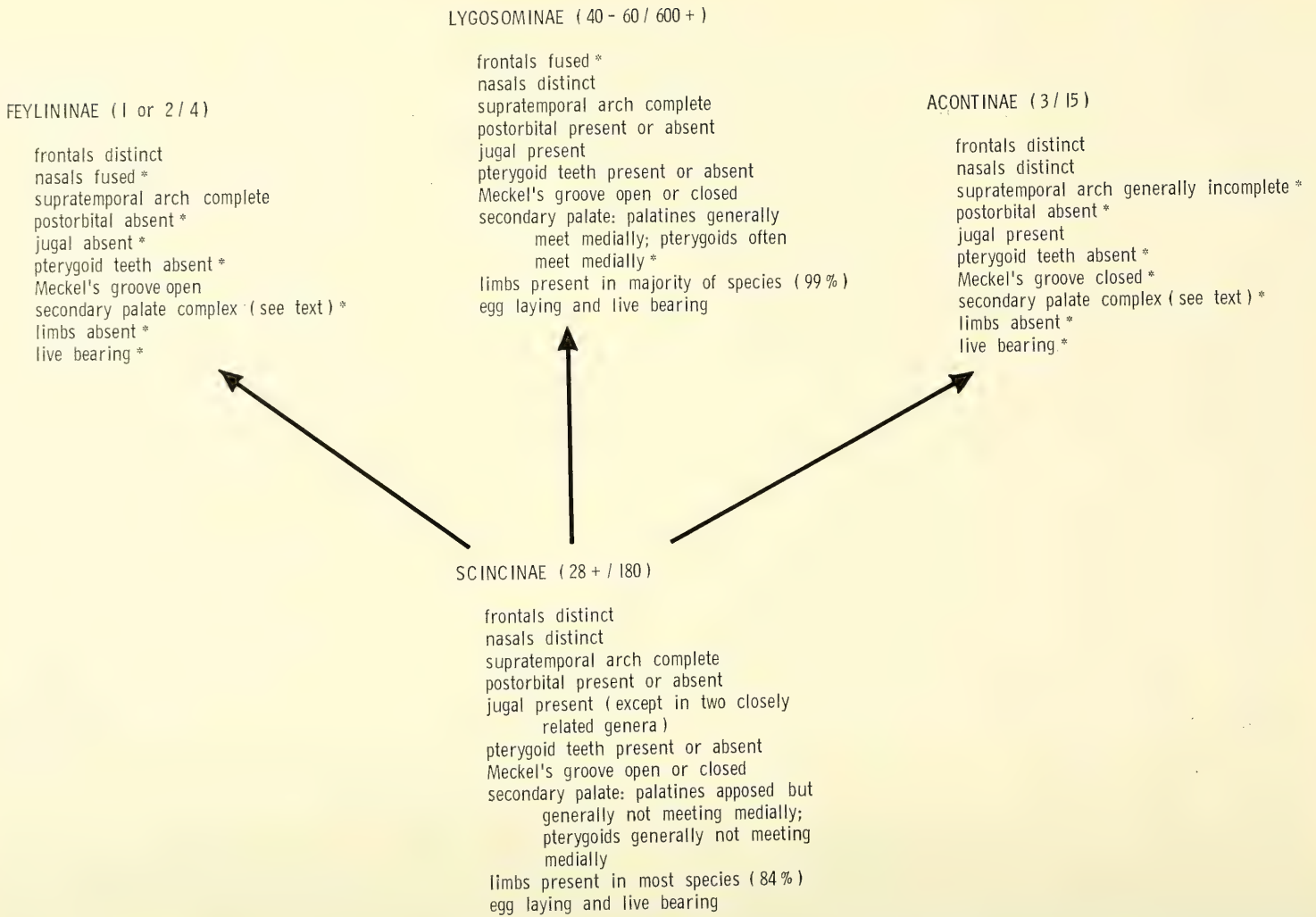

Figure 7. Hypothetical phylogeny of the four subfamilies of skinks. Derived character states are indicated by an asterisk (*). The number of genera and species for each taxon are given in parentheses on the left and right sides of the slash mark.

these aberrant species belong are quite closely related, the diversity in morphology and behavior displayed by these species (within the group formed by the two genera) leads me to view them more as distantly related end products, in which the palatines have secondarily separated, than as a closely knit, basal lygosomine stock retaining the primitive scincine palate.

Similarly, the few scincines with only the palatines meeting medially (*Proscelotes* and *Scelotes*) appear to be a monophyletic group and could be viewed, on the basis of this character, as being either immediately ancestral to the lygosomines or independently specialized scincines. Although it is difficult to make a decision between these two hypotheses, my feeling is that the latter hypothesis is correct.

It seems fairly clear, however, that the three endemic scincine Seychelles "*Scelotes*" and the Mauritian scincine *Gongylomorphus bojeri* have, as a group,[1] independently evolved a very advanced, complete secondary palate involving both the palatine and pterygoid bones. If this were not the case, and these four species were to be considered as ancestral to the lygosomines, then we would have to look upon those lygosomines with the palatines and pterygoids meeting medially as being primitive, and the lygosomines with only the palatines either meeting medially or separated as advanced. Such a hypothetical developmental sequence, however, has no evidence whatsoever to support it and is, in fact, refuted by the ontogenetic and fossil evidence discussed above. To believe this hypothesis would require us to throw out the only evidence we have on the evolution of the secondary palate in skinks and to accept the hypothetical alternative purely on faith.[2]

It would seem, then, that a complete secondary palate has evolved from an incomplete secondary palate at least twice and perhaps three times in skinks: once in the lygosomines (concomitant with the fusion of the frontals) and once or twice in the scincines (depending on the as yet unanswered question of whether the complete secondary palate in the *Proscelotes-Scelotes* group and the Seychelles "*Scelotes*"-*Gongylomorphus bojeri* group is due to relationship or convergence).

It thus seems fairly clear that scincines are ancestral to lygosomines, but we have yet to place the feylinines and acontines in the phylogeny of the subfamilies. These two groups are highly specialized burrowers and are unlikely to have been ancestral to any major group of skinks living today. Their divided frontals and incomplete secondary palates align them much more closely with the scincines than with the lygosomines. This notion is further supported by the fact that both acontines and feylinines are limbless, and it has been the scincines more than the lygosomines that have tended to lose the limbs entirely.

The secondary palates of the acontines and feylinines are extremely complex and extremely unlike each other, which makes it seem very probable that the two taxa arose independently from a scincine ancestry. It is difficult to distinguish the scincine relatives of the acontines, but the scincine *Typhlacontias* and *Fitzsimonsia*,

[1] On the basis of other characters, as well as the relationships of the bones of the palate, the endemic Seychelles "*Scelotes*" and the Mauritian *Gongylomorphus bojeri* appear to be each other's closest relatives and form a monophyletic group. This relationship and its interesting zoogeographic implications will be discussed elsewhere.

[2] I intend to refute this hypothesis only as a broad explanation of the evolution of the secondary palate in skinks. Minor "reversals" in the general trend from an incomplete secondary palate to a complete and ever more extensive secondary palate might be expected and would not be strong enough evidence, in my mind, to offset the ontogenetic and fossil evidence in favor of this general trend. Indeed, as suggested above, it seems possible that such a minor "reversal" in the general trend is what we see in the incomplete secondary palates of a few lygosomines (most *Egernia* and *Corucia zebrata*).

with their peculiar stapes-quadrate articulation (see page 163), and the absence of the jugal bone, are similar to the feylinines. However, this similarity may well be the result of convergence (both taxa are burrowers) rather than relationship.

The data discussed in this section are summarized in the phylogenetic tree of Figure 7.

ZOOGEOGRAPHY OF THE MAJOR TAXA OF SKINKS

The zoogeography of the major taxa of skinks can be readily understood on the basis of the morphological and distributional data for the many living and very few fossil species summarized in the preceding sections of the paper.

Basic to the following discussion is the idea developed above that the scincines have given rise independently to the other three major groups of skinks, the Feylininae, Acontinae, and the most speciose and morphologically "advanced" group of skinks, the Lygosominae. The present distribution of the four subfamilies of skinks seems to support this broad phylogenetic hypothesis.

With the exception of *Eumeces* (the largest genus in the subfamily, 46 species) and the monotypic *Neoseps* of Florida, the Scincinae are entirely Old World in distribution and, again with the exception of the widespread *Eumeces*, show a relict distribution in south central and eastern Asia (Fig. 4). For example, the only scincine, with the exception of *Eumeces*, in eastern Asia is *Brachymeles* (13 species) in the Philippines. As one moves west through Asia, no other scincines are encountered until, on reaching India, the monotypic *Barkudia* is known from the regions around Chilka Lake and Calcutta. Further south in India there is a single species of *Sepsophis* in the central and southern part of the subcontinent and two endemic genera, *Nessia* (8 species) and *Chalcidoseps* (1 species), on Ceylon.

It is not until one reaches southwest Asia and the Mediterranean area that one encounters widely distributed genera with many species, e.g., *Ophiomorus* (9 species), *Scincus* (12 species), and *Chalcides* (14 species). It is south of the Sahara Desert in Africa, Madagascar, and the islands of the western Indian Ocean that the scincines become an important part of the skink fauna (76 of the 136 species of non-*Eumeces* scincines occur in this area).

Two of the other three subfamilies are also found in subsaharan Africa. The Acontinae, with approximately 15 species, and the Feylininae, with 4 species, are undoubtedly derived from scincines in Africa; this, along with the present large number of species and their extensive distribution in subsaharan Africa, Madagascar, and the islands of the western Indian Ocean, appears to indicate that the scincines have been in subsaharan Africa for much, if not most, of their evolutionary history.

Whether the scincines were ever in the Australian Region is an interesting question. The furthest east scincines range in the Old World today is the Philippines (*Brachymeles*, 13 species). It is, of course, possible that the scincines have been completely replaced in the Australian Region by the lygosomines, although the total absence of any scincine relicts in Australia or the numerous island groups of the Region makes me believe that the scincines never reached this part of the world.

The reasons for the relict distribution of the scincines in south and east Asia and their abundance in southwest Asia, Africa, and Madagascar are undoubtedly complex but may be due in part to the evolution and radiation of the Lygosominae in southeast Asia and the Australian Region. The lygosomines are clearly derived from scincines and are morphologically the most advanced skinks. This group is most numerous and diverse in southeast Asia and the Australian Region, and its expansion from this area of origin may account in part for the relict distribution of the scincines in south and east Asia. In southwest Asia,

Africa, and Madagascar, the area of the Old World furthest from their area of origin, the lygosomines are fairly well represented by species, but they are not morphologically diverse (i.e., there are not many genera). Presumably the lygosomines are only recent arrivals in this area and have not yet swamped their ancestral scincine relatives. Perhaps if we could return in several million years, the scincines would show a relict distribution in Africa, Madagascar, and the islands of the west Indian Ocean as they do in southern and eastern Asia today.

The overall geographic picture of skink evolution in the Old World is distinctly bipolar. The scincines appear to have had a long evolutionary history in Africa, giving rise to numerous genera and species as well as to two other subfamilies of skinks, whereas the spectacular radiation of the more advanced lygosomines appear to be predominately a phenomenon of the Australian Region—an area that was probably never reached by the scincines.

The origin of the New World skink fauna is of special interest. In view of the great diversity and abundance of skinks in the Old World, the most remarkable aspect of the New World skink fauna is its paucity. This, plus the fact that three of the four genera in the New World are also widespread in the Old World, indicates that the Old and not the New World is surely the ancestral home of the family.

Eumeces is represented by 31 species in the New World and 15 in the Old World. The genus has been in North America at least since the late Oligocene (see Fossil Record of Skinks, above) and in that time has successfully rafted to Bermuda (*E. longirostris*), but, peculiarly, the group has not spread further south than Costa Rica.

Eumeces undoubtedly arrived in the New World via a Bering Land Bridge. The group is very primitive even for scincines[1] (Greer, in preparation), and its distribution along the northern periphery of the range of skinks in the Old World (Fig. 5) implies a greater cold tolerance than in most other skinks. In both time and place, therefore, *Eumeces* would have been in a good position to take advantage of a Bering Land Bridge.

The relationships of the New World *Leiolopisma* with each other and with their supposed Old World congeners is a major unsolved problem in skink systematics. For the moment I am treating the *Leiolopisma* of the New World as congeneric with a group of southeast and east Asian *Leiolopisma*. In east Asia, this group ranges as far north as about 41°N lat., which is only slightly further south than the northern limit of the range of *Eumeces* in Asia (about 45°N lat.). Thus, like *Eumeces*, these *Leiolopisma* would be "cold tolerant" enough to have taken advantage of the Bering Land Bridge during slightly warmer times.

There is no fossil record for *Leiolopisma* in the New World, so the time of arrival of the group is unknown, but the few species in the New World and their absence from islands like Bermuda may indicate that the group arrived in North America after *Eumeces*. Like *Eumeces*, however, *Leiolopisma* has not entered South America, although it is known as far south as Panama.

The fact that both *Eumeces* and *Leiolopisma* come so close, but fail to enter South America, seems a bit peculiar to me and merits further discussion. The water gap that persisted through most of the Tertiary across Panama and northern

[1] Morphologically *Eumeces* is very possibly the most primitive living skink taxon and may, in fact, be quite similar to the ancestor of all skinks. In view of this primitiveness, it might seem peculiar that the group should be so successful—if number of species is acceptable as a criterion for success (*Eumeces*, with about 46 species, is the most speciose genus of scincines). But the primitiveness discussed here is morphological, and on other characters, such as the maternal care of the eggs, *Eumeces* shows the greatest advancement of any lizard for which such data are available.

Colombia probably aided in excluding both genera from South America, but this cannot be the whole answer, as skinks have few peers among squamates in crossing water barriers and, regardless of the Tertiary water gap, both genera have had ample time since the closure of the isthmus to enter South America (as has apparently been the case with the genus *Rana* and the two genera of Bolitoglossine salamanders).

Competitive exclusion by resident South American lizards filling niches similar to those filled by *Leiolopisma* and *Eumeces* may be of as great importance in explaining the absence of these two genera from South America as is the Panamanian-Colombian water gap. For example, the micro-teiids, which probably arose in South America and have only recently invaded Central America, are very skink-like in their external morphology and habits and may be South America's candidate for the skink niche (along with the endemic *Mabuya*).

The genus *Mabuya* is currently thought to comprise approximately nine species in the New World (Dunn, 1936), although this estimate may be low. These species are distributed throughout South America, the West Indies, Central America, and Mexico as far north as Veracruz and Colima. The lack of diversity of the New World species may indicate that the group has not been in the New World very long. There are many *Mabuya* both in Asia and Africa, so it is difficult to decide whether the group arrived from Asia via the Bering Land Bridge or from Africa by over-water rafting. Three bits of evidence make me favor the latter possibility. First, the genus is very good at crossing water gaps, as evidenced by the endemic *Mabuya* of the Cape Verde Islands, Madagascar, the Seychelles, and Fernando de Noronha and the *Mabuya* of the West Indies. Second, there are no *Mabuya* in the southeastern United States, unlike the case with many Asian immigrants (*Magnolia*, pattlefishes, *Ophisaurus*, *Leiolopisma* and *Eumeces*). And third, there are endemic South American and West Indian species of other African lizard genera (*Lygodactylus*, *Tarentola*) whose ancestors almost surely arrived in the New World across the Atlantic. Also, Dunn (1936) thinks that "the nearest relationship of the mainland and Caribbean forms [of *Mabuya*] seems to be with the mainland African species of the *raddoni-affinis* group."

The fourth group of New World skinks is the monotypic scincine genus *Neoseps* of peninsular Florida. *Neoseps* is an attenuate burrower in sandy loamy soil and presents no great zoogeographic problem, as it has probably simply evolved from a *Eumeces* ancestor *in situ* (Telford, 1959). Not only is there a close morphological similarity between the two genera (Greer, personal observation), but they are also the only skinks yet known in which the female guards the eggs.

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Mr. Arnold Clapman drew the skulls for Figures 1 and 2.

LITERATURE CITED

Ali, S. M. 1947. The dermal scutes of *Mabuya dissimilis* Hallowell. Curr. Sci. **16:** 348.

Angel, F. 1942. Les lézards de Madagascar. Mémoires de l'Académie Malgache **36:** 1–193.

Boulenger, G. A. 1887. Catalogue of the lizards in the British Museum (Natural History). Vol. III, 2nd ed., London, Taylor and Francis, xii + 575 pp.

Brock, G. T. 1941. The skull of *Acontias meleagris*, with a study of the affinities between lizards and snakes. J. Linn. Soc. (Zool.) **41:** 71–88.

Brühl, C. B. 1886. Zootomie aller Thierklassen für Lernende, nach Autopsien, skizzert. Lief. **38.** Vienna, Alfred Hölder.

Cope, E. D. 1892. The osteology of the Lacertilia. Proc. Amer. Phil. Soc. **3:** 185–221.

Deraniyagala, P. E. P. 1953. A colored atlas of some vertebrates from Ceylon. Vol. II. Tetrapod Reptilia. Ceylon National Museums Publication, Ceylon Govt. Press, 101 pp.

———. 1960. Some osteological characters of the apodal skink *Anguicephalus hickanala* Deraniyagala. Spolia Zeylan. **29:** 29–32.

Duméril, A., and M. F. Bocourt. 1881. Mission scientifique au Mexique et dans l'Amérique Centrale. Part **3**(7): 441–488.

Dunn, E. R. 1936. Notes on American Mabuyas. Proc. Acad. Nat. Sci. Philadelphia. **87:**533–557.

El-Toubi, M. R. 1938. The osteology of the lizard *Scincus scincus* (Linn.). Bull. Fac. Sci. Egyptian Univ. (Cairo) **14:**1–38.

Essex, R. 1928. Studies in reptilian degeneration. Proc. Zool. Soc. London, 1927, part 4:879–945.

Estes, R. 1963. Early Miocene salamanders and lizards from Florida. Quart. J. Florida Acad. Sci. **26:**234–256.

———. 1964a. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. Univ. California Publ. Geol. Sci. **49:** 1–180.

———. 1964b. Notes on some Paleocene lizards. Copeia **1965**(1):104–106.

Estes, R., and J. A. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska. American Midl. Nat. **72**(2):453–472.

Etheridge, R. 1967. Lizard caudal vertebrae. Copeia **1967**(4):699–721.

Fitch, H. S. 1954. Life history and ecology of the Five-lined Skink, *Eumeces fasciatus*. Univ. Kansas Mus. Nat. Hist. Publ. **8**(1): 1–156.

Ganapati, P. N., and K. Rajyalakshmi. 1958. Bionomics and some anatomical peculiarities of the limbless lizard *Barkudia insularis* Annandale. Rec. Indian Mus. **53:**279–291.

Gosse, P. H. 1848. On the habits of *Mabouya agilis*. Proc. Zool. Soc. London **16:**59–62.

Greer, A. E. 1967a. A new generic arrangement for some Australian scincid lizards. Breviora No. **267:**1–19.

———. 1967b. The relationships of the African scincid genus *Eumecia*. Breviora No. **276**: 1–9.

Greer, A. E., and F. Parker. 1967. A new scincid lizard from the northern Solomon Islands. Breviora No. **275**:1–20.

———, ———. 1968. *Geomyersia glabra*, a new genus and species of scincid lizard from Bougainville, Solomon Islands, with comments on the relationships of some lygosomine genera. Breviora No. **302**:1–17.

Haas, G. 1935. Zum Bau des Primordialcraniums und des Kopfskelettes von *Ablepharus pannonicus*. Acta Zool. **16**:409–429.

———. 1936. Ueber das Kopfskelett von *Chalcides guentheri* (*Seps monodactylus*). Acta Zool. **17**:55–74.

Hewitt, J. 1929. On some Scincidae from South Africa, Madagascar and Ceylon. Ann. Transvaal Mus. **13**(1):1–8.

Hoffstetter, R. 1944. Sur les Scincidae fossiles. I. Formes européennes et nord-américaines. Bull. Mus. Natl. Hist. Nat. (2)**16**(6):547–553.

———. 1945. Sur les Scincidae fossiles. II. Formes subfossiles de L'Île Maurice. Bull. Mus. Natl. Hist. Nat. (2)**17**(1):80–86.

———. 1949. Les reptiles subfossiles de L'Île Maurice. I. Les Scincidae. Annales de Paléontologie **35**:45–72.

———. 1961. Squamates. *In*: Le gisement de vertébrés Miocènes de Beni Mellal (Maroc). Notes Mém. Serv. Géol. Maroc **155**:95–101.

———. 1962. Revue des récentes acquisitions concernant l'histoire et la systématique des squamates. *In*: Problems actuels de paléontologie (évolution des vertébrés). Coll. Intern. Centre Nat. Rech. Scient. **104**:243–279.

Kamel, A. E. 1965. The cranial osteology of adult *Chalcides ocellatus*. Anat. Anz. **117**: 338–370.

King, D. 1964. The osteology of the water skink *Lygosoma* (*Sphenomorphus*) *quoyii*. Aust. J. Zool. **12**:201–216.

Kingman, R. H. 1932. A comparative study of the skull in the genus *Eumeces* of the family Scincidae. Univ. Kansas Sci. Bull. **20**(15): 273–295.

Loveridge, A. 1957. A check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). Bull. Mus. Comp. Zool. **117**(2):153–362.

Merwe, N. J. van de. 1944. Die Skedelmorfologie van *Acontias meleagris* (Linn.). Tydskrif vir Wetenskap en Kuns, vol. number not available: 59–88.

Miller, M. R. 1966a. The cochlear duct of lizards. Proc. Calif. Acad. Sci. **33**(11):255–359.

———. 1966b. The cochlear ducts of *Lanthanotus* and *Anelytropsis* with remarks on the familial relationship between *Anelytropsis* and *Dibamus*. Occ. Pap. Calif. Acad. Sci. No. **60**: 1–15.

Mitchell, F. J. 1950. The scincid genera *Egernia* and *Tiliqua* (Lacertilia). Rec. South Aust. Mus. **9**(3):275–308.

Mittleman, M. B. 1952. A generic synopsis of the lizards of the subfamily Lygosominae. Smithsonian Misc. Coll. **117**(17):1–35.

Oliver, J. A. 1951. Ontogenetic changes in osteodermal ornamentation in skinks. Copeia **1951** (2):127–130.

Otto, H. 1908. Die Beschuppung der Brevilinguier und Ascalaboten. Jena. Zeitschr. Naturwiss. **54**(37):1–61.

Pearson, H. S. 1921. The skull and some related structures of a late embryo of *Lygosoma*. J. Anat. London **56**:20–43.

Peters, W. C. H. 1882. Reise nach Mossambique. Zoologie. III. Amphibien. G. Reimer, Berlin, x + 191 pp., 26 pls.

Rabanus, K. 1911. Über das Skelett von *Voeltzkowia mira* Bttgr. *In*: A. Voeltzkow, Reise in Ostafrika. Wiss. Ergebn. **4**:279–330.

Rao, M. K. M., and L. S. Ramaswami. 1952. The fully formed chondrocranium of *Mabuya* with an account of the adult osteocranium. Acta Zool. **33**:209–275.

Rathore, M. S. 1967. The bionomics and anatomy of *Ophiomorus tridactylus* (Blyth) Boulenger. Ph.D. Thesis, University of Rajasthan, Jaipur, India.

Rice, E. L. 1920. The development of the skull in the skink *Eumeces quinquelineatus* L. J. Morph. **24**:119–220.

Romer, A. S. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press, xxi + 772 pp.

Sibtain, S. M. 1938 Studies on the caudal autotomy and regeneration in *Mabuya dissimilis* Hallowell. Proc. Indian Acad. Sci. **13**(1): 63–78.

Siebenrock, F. 1892. Zur Kenntniss des Kopfskelettes der Scincoiden, Anguiden und Gerrhosauriden. Ann. naturhist. Mus. Wien **7** (3):163–196.

Smith, M. A. 1935. The Fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. Vol. II. Sauria. London, Taylor and Francis, xii + 440 pp.

———. 1937. A review of the genus *Lygosoma* (Scincidae: Reptilia) and its allies. Rec. Indian Mus. **39**(3):213–234.

Taylor, E. H. 1941. Extinct lizards from Upper Pliocene deposits of Kansas. Univ. Kansas Publ., State Geol. Surv. Kansas, Bull. **38**, Rep. of Studies, Pt. 5:165–176.

Telford, S. R. 1959. A study of the sand skink, *Neoseps reynoldsi* Stejneger. Copeia **1959** (2):110–119.

Tilak, R., and S. C. Rastogi. 1964. Dermal scutes in Sauria (Reptilia). Proc. Zool. Soc. Calcutta **17**:183–191.

Twente, J. W. 1952. Pliocene lizards from Kansas. Copeia **1952**(2):70–73.

Villiers, C. G. S. de. 1939. Über den Schädel des südafrikanischen schlangenartigen Scinciden *Acontias meleagris*. Anat. Anz. **88**: 320–347.

Waite, E. R. 1929. The reptiles and amphibians of South Australia. Adelaide, Harrison Weir, Govt. Printer, 270 pp.

Witte, G. F. de. 1953. Exploration du Parc National de l'Upemba. Reptiles. Institut des Parcs Nationaux du Congo Belge, Fasc. **6**: 1–322.

Witte, G. F. de, and R. Laurent. 1943. Contribution a la systématique des formes dégradées de la famille des Scincidae apparentées au genre *Scelotes* Fitzinger. Mém. Mus. Roy. Hist. Natur. Belgique, sér. 2, fasc. **26**:1–44.

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New Species of Bottom-Living Calanoid Copepods Collected in Deepwater by the DSRV Alvin

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NEW SPECIES OF BOTTOM-LIVING CALANOID COPEPODS COLLECTED IN DEEPWATER BY THE DSRV ALVIN[1]

GEORGE D. GRICE[2] AND KUNI HÜLSEMANN[3]

ABSTRACT

The use of a deep sea submersible for collecting near bottom copepods is described. Thirteen new species of calanoid copepods were found in a plankton sample collected within 30 cm of the bottom at a depth of approximately 1800 meters on the continental slope south of Woods Hole, Massachusetts. The species are described and illustrated.

INTRODUCTION

Several families of calanoid copepods have species which live in proximity to the bottom. These species, termed planktobenthos by Hutchinson (1967), are not usually collected in abundance by ordinary plankton collecting techniques, as it is not prudent to permit a towed plankton net to get very near to the bottom, especially in deepwater, where it might be fouled, torn or lost. Specialized collecting apparatus have been devised for collecting animals that live near the seabed. Matthews (1964) described three types of gear that he used to sample bottom-living calanoid copepods which he referred to as epibenthos, at a depth of 240 m south of Bergen, Norway. In addition to Matthews' methods, planktobenthos have also been collected by attaching a tow net above a bottom dredge or to a bottom trawl as Farran (1905), for example, did in his investigations of the copepods of the slope area off Ireland. Farran's deepest bottom plankton collection was obtained by a trawl in 382 fathoms. Frolander and Pratt (1962) have described a "bottom skimmer" which they used for collecting planktobenthos at a depth of 40 feet in a lake.

The recent acquisition of the Deep Submergence Research Vehicle ALVIN by the Woods Hole Oceanographic Institution provided us with a means to sample planktobenthos with greater precision and in greater depths than we believe to have been hitherto practical. With plankton nets attached to ALVIN as shown in Figures 1 and 2, the pilot, by visual observation, can keep the nets just above the bottom for prolonged sampling periods in depths down to approximately 1900 m, the maximum operational depth of ALVIN.

SAMPLING PROCEDURE

In the initial attempt to sample the planktobenthos from ALVIN, samples were collected by means of two nets attached to the submersible. The mouth opening of the nets (.233 mm aperture size) were "D" shaped with the straight side fastened

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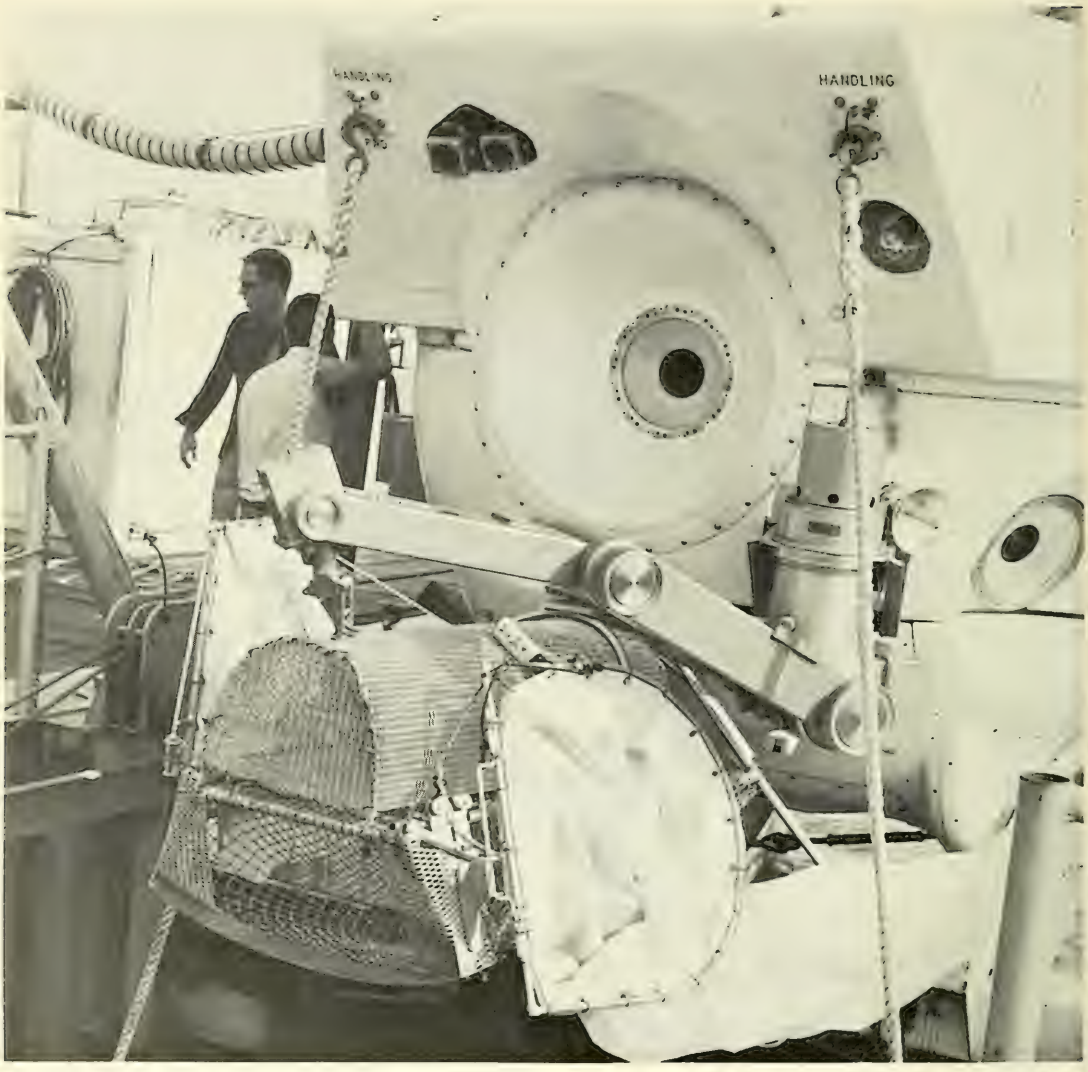

Figure 1. Position of plankton nets during descent of ALVIN.

vertically to a hinge located on the forward end of the submersible's collecting basket (Figs. 1, 2). During the descent of the submersible, the mouth was held sideways (Fig. 1) in order to reduce the possibility of obtaining plankton while on the way to the bottom. Upon reaching the bottom, the mechanical arm of ALVIN was used to swing the mouth of one net into the sampling position (Fig. 2) and to hold it there for the duration of the sampling period. The net was kept within 30 cm of the bottom while the submersible cruised at approximately 1 1/2 knots. At the end of one hour the mouth was allowed to swing back to its original position and the pursing line was tightly drawn around the net by means of the mechanical arm. The other net was then opened and a sample collected in the same manner as described for the first net. The collections were obtained by Dr. Howard Sanders and his associates.

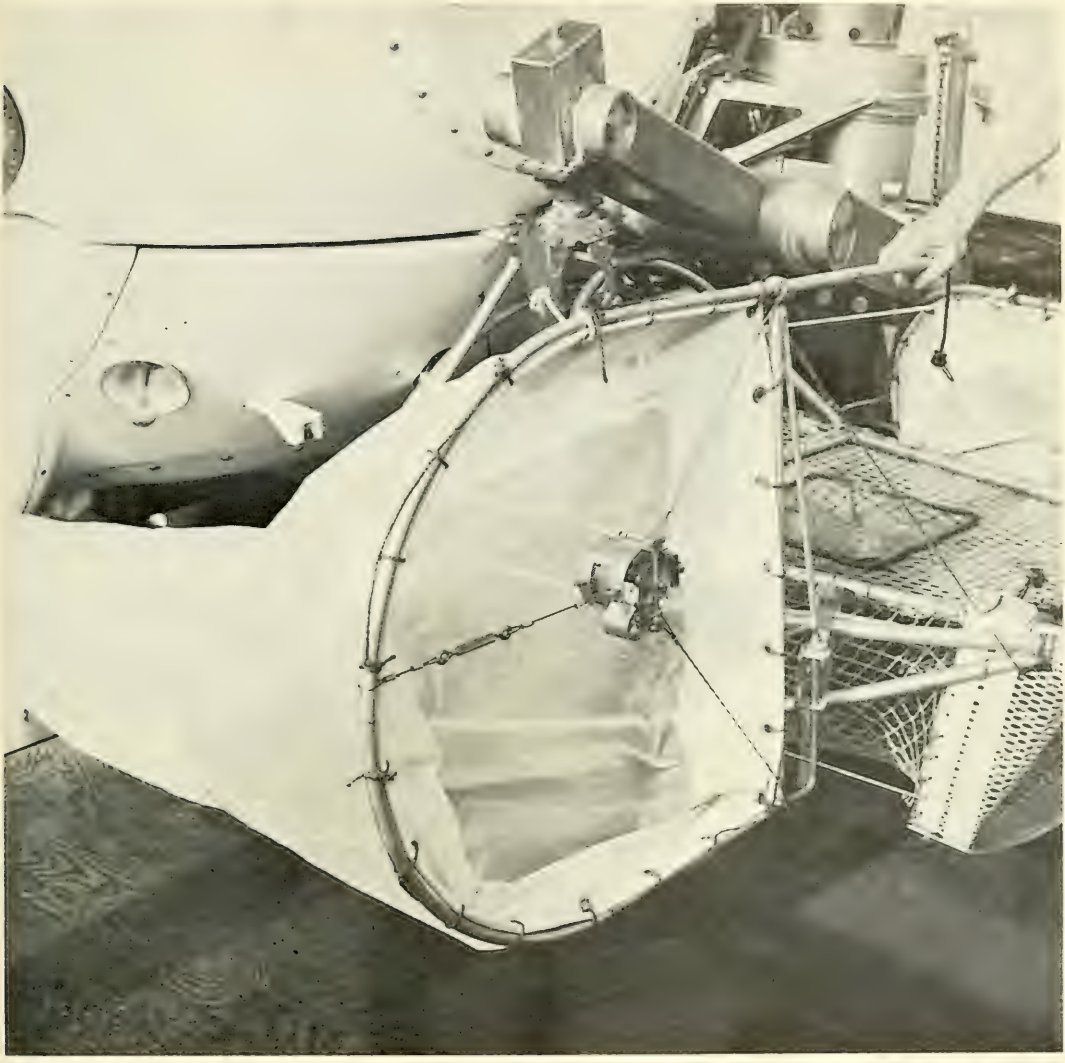

Figure 2. One plankton net in sampling position.

DESCRIPTION OF COLLECTING AREA

The collections were made south of Woods Hole, Massachusetts, at 39°45.2′N 70°33.8′W on September 19, 1967 (ALVIN Dive 220). The water depth in the area varied between 1750 and 1822 m and the temperature was 3°C. The bottom was composed of fine sediment with a flocculent zone at the surface which was readily stirred up. A slight current was noticeable near the bottom.

RESULTS

Since the two samples came from approximately the same depths and since the bottom topography appeared homogeneous in the area, the two are here treated as one. Sixty-five species of calanoid copepods were identified, including 13 new species that will be described below.

These 13 species with the possible exception of *Aetideopsis magna*, probably live in proximity to the seabed. From

dredge collections made near Norway, Sars (1902) described bottom-living species of *Bryaxis* (= *Comantenna*), *Diaixis*, *Tharybis*, and *Xanthocalanus*, the first three being established as new genera. Except for *Tharybis*, we encountered undescribed species referable to these genera. *Tharybis* is now considered to be one of three genera in the Family Tharybidae. We found undescribed species of the other two genera of Tharybidae, *Undinella* and *Parundinella*. *Comantenna* is closely associated with the seabed (Matthews, 1964), as are some species of *Xanthocalanus* (Sars, 1925). Species of *Amallophora*, of which we found two undescribed ones, have not been taken in abundance in mid-water plankton samples. Perhaps this genus, too, has bottom affinities.

Representatives of typically planktonic species were also noted and include, for example, *Calanus finmarchicus*, *C. hyperboreus*, *Eucalanus elongatus*, *Clausocalanus furcatus*, *Microcalanus pygmaeus*, *Pseudocalanus elongatus*, *Temoropia mayumbaensis*, *Metridia curticauda*, *Pleuromamma robusta*, *Centropages typicus*, and *Acartia danae*. Some of these may have entered the net during the descent of the submersible. As may be noted in Figure 2, the net is folded back (not pursed) during this phase of the collection. However, several of these very same species together with some others were reported from samples collected just over the sea floor by Matthews (1964) in his study on bottom-living copepods off western Norway.

Type specimens have been deposited in the U. S. National Museum.

FAMILY AETIDEIDAE

Aetideopsis magna n. sp.
Pl. I, figs. 3–19

Material examined: 6 males

Diagnosis (male). Head and first thoracic segment fused, fourth and fifth thoracic segments partially fused. Abdomen consisting of five segments, second segment largest, anal segment very short. Rostrum 2-pointed, small. Posterolateral margin of fifth thoracic segment more or less rounded with posteriorly directed small spine. Antennule reaching third thoracic segment. In right antennule segments 8 and 9, 20 and 21 fused; in left antennule segments 8 and 9 only fused. Large aesthetasks on segments 2 to 9. Exopod of antenna shorter than endopod. Basal segment of mandible palpus devoid of setae. Mandible blade rudimentary. Maxillule and maxilla reduced. Second basipodal segment of maxillipod slender, slightly longer than first. Endopod of first leg 1-segmented, of second leg 2-segmented, of fourth leg 3-segmented. Exopod of first leg 3-segmented, of other legs broken short. Posterior side of second and fourth legs with patches of short hair. Fifth legs asymmetrical, left side longer than right. Endopods slender, 1-segmented. Exopod of right fifth leg ending with slender point. Second exopodal segment of left fifth leg with setae distally, third segment small, with hair at tip. Total lengths 4.20–4.56 mm. Holotype No. 125135.

The female is unknown.

Remarks. Aetideopsis magna resembles *A. multiserrata* (Wolfenden), but is distinguished by its larger size, the relatively shorter spine in the fifth thoracic segment, and the longer left fifth leg. No female belonging to this genus was found in the sample.

The name *magna* refers to the relative size of this species.

Comantenna recurvata n. sp.
Pl. I, figs. 20–24; Pl. II, figs. 25–35

Material examined: 4 females

Diagnosis (female). Head and first thoracic segment fused. Fourth and fifth thoracic segments separate. Abdomen 4-segmented, anal segment small. Rostrum absent. Posterolateral corners of cephalothorax pointed and curved upward. Antennules 23-segmented, reaching to third thoracic segment. Antennules with numer-

ous, highly plumose setae throughout their length and 1 sensory seta on the second segment. Exopod of antenna three-fourths the length of endopod. Distal segment of exopod with 2 long and 1 short plumose setae. Endopod of mandible very small, exopod robust. Mandible blade with strong teeth and scattered spines. Maxillule with 14 spines on first inner lobe, 4 setae on second inner lobe, 3 setae on third inner lobe, 4 setae on second basal segment, 11 setae on endopod, and 11 setae on exopod. Maxilla with 5 lobes. Maxilliped with elongate, club-shaped sensory structure arising from distal end of first basal segment. Exopods of swimming legs 3-segmented, endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented. Rudimentary fifth legs present on 2 of 4 specimens. Total lengths 3.72–4.00 mm. Holotype No. 125136.

The male is unknown.

Remarks. The large size of the present species and the presence of long plumose setae on the terminal segment of the exopod of the antenna will distinguish it from *C. brevicornis* (Sars). This latter species, known from the Northeast Atlantic (near the bottom) is smaller (1.7–2.6 mm) and has poorly developed terminal setae on the distal segment of the exopod of the antennae. In other respects the two species closely resemble each other and, with the finding of additional specimens in shallower depths in the Northeast Atlantic, may prove to be conspecific. *C. brevicornis* has been collected off Norway in bottom samples to depths of about 300 m.

The specific name *recurvata* refers to the shape of the points on the posterior end of the cephalothorax.

FAMILY PHAENNIDAE

Xanthocalanus alvinae n. sp.

Pl. II, figs. 36–40; Pl. III, figs. 41–54

Material examined: 5 females

Diagnosis (female). Cephalothorax slender. Head and first thoracic segment fused, but trace of segmentation visible. Fourth and fifth thoracic segments separate. Abdomen 4-segmented, anal segment very short. Rostrum with two filaments of moderate length. Posterolateral corner of fifth thoracic segment angular, little produced. Antennules with 22 free segments, segments 8–10 and 24 and 25 fused; reaching end of third abdominal segment. Exopod of antenna consisting of 7 segments, slightly longer than endopod. Basal segment of mandible palpus carrying 3 setae, mandible blade with rather simple teeth. Two setae on second inner lobe of maxillule, 4 setae on third inner lobe, 4 setae on second basal segment, 2 and 5 setae on endopod, 7 setae on exopod. First lobe of maxilla with 3, second to fourth lobes with 2, fifth lobe with 3 setae, one of them spinelike, and a sensory appendage; endopod carrying sensory filaments. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs and exopods of first to third legs 3-segmented, exopod of fourth leg broken. Posterior sides of both rami of second and third legs spinulose, of endopod of fourth leg covered with hairlike spines. Fifth leg composed of 3 segments of about equal length equipped with conspicuous hair and spinules. Second segment slightly wider than long, distal segment carrying 1 external, 1 internal, and 1 terminal spine, the latter being the shortest. One female had 2 terminal spines. Internal spine strong, exceeding distal segment in length, directed more or less at right angle to segment. Total lengths 2.10–2.34 mm. Holotype No. 125137.

Remarks. Xanthocalanus alvinae closely resembles *X. echinatus* Sars. It can, however, be distinguished by its fifth leg which is 3-segmented, has dense, long hair on the second segment and 1 (or 2) jointed terminal spines on the distal segment. The fifth leg of *X. echinatus* is 2-segmented, the short proximal segment is devoid of hair, and the distal segment ends in a conical protrusion.

The male is unknown.

This species is named for the DSRV ALVIN.

Xanthocalanus distinctus n. sp.
Pl. III, figs. 55–57; Pl. IV, figs. 58–73

Material examined: 3 males

Diagnosis (male). Head and first thoracic segment incompletely fused. Fourth and fifth thoracic segments separate. Abdomen 5-segmented, anal segment very short. Rostrum well developed with 2 filaments. Posterolateral margin of fifth thoracic segment angular. Antennule reaching end of furca, segments 8–12 and 13 and 14 fused. Endopod of antenna slightly shorter than exopod. Basal segment of mandible palpus with 2 setae; blade with a number of complex teeth. In maxillule 2 setae on second inner lobe, 4 setae on third inner lobe, 4 setae on second basal segment, 2 and 5 setae on endopod, 7 setae on exopod. Fifth lobe of maxilla with strong spine; third and fourth lobe each with 1 sensory appendage. Endopod carrying 2 types of sensory filaments. Basipods of maxilliped nearly equal in size, second segment of endopod longest. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs as well as exopods of first to fourth legs 3-segmented. Posterior sides of most of second to fourth legs covered with spinules and hair. Fifth legs asymmetrical, left side about 3 times the length of right side. Both sides 5-segmented, endopods absent. Total lengths 2.44–2.56 mm. Holotype No. 125138.

The female is unknown.

Remarks. The male of *Xanthocalanus distinctus* resembles the male of *X. fallax* Sars. It differs, however, in the separate fourth and fifth thoracic segment, the longer antennule, and the relatively longer right fifth leg. In *X. fallax*, the fourth and fifth thoracic segments are fused, the antennule overreaches the end of the thorax only slightly, and the right fifth leg is only about one-fourth of the length of the left leg.

The meaning of the name of this species is obvious.

Xanthocalanus elongatus n. sp.
Pl. IV, figs. 74–78; Pl. V, figs. 79–96; Pl. VI, figs. 97–110

Material examined: 25 females, 17 males

Diagnosis (female). Head and first thoracic segment fused, fourth and fifth thoracic segments separate. Abdomen 4-segmented. Genital segment with short hair mainly distributed on sides and posterior margin; anal segment very short. Rostrum of moderate size with 2 filaments. Posterolateral margin with small point. Antennule reaching to middle of genital segment; composed of 24 free segments, segments 8 and 9 fused. Endopod of antenna nearly as long as exopod. Basal segment of mandible palpus bearing 3 setae; blade with 8 teeth and 1 seta. In maxillule, 2 setae on second inner lobe, 3 setae on third inner lobe, 5 setae on second basal segment, 3 and 5 setae on endopod, 7 setae on exopod. Fifth lobe with 2 strong spines and 1 seta; 1 seta each modified as sensory structure on third and fifth lobes. Endopod with 3 ribbonlike and 5 smaller sensory appendages. First and second basal segments of maxilliped of about equal length, in endopod second segment longest. Endopods of first leg 1-segmented, of second leg 2-segmented, of third and fourth as well as exopods of first to fourth legs 3-segmented. Posterior sides of rami of second to fourth legs covered with spinules, especially dense on fourth leg including both basipodal segments. Fifth leg 3-segmented, second and third segments with many spinules mainly on outer side. Distal segment with 1 short terminal and 1 long internal spine. Internal spine inserting close to terminal spine, exceeding distal segment of fifth leg in length.

Total lengths (12 females) 2.48–2.80 mm. Holotype No. 125139.

Diagnosis (male). Head and first thoracic segment fused, fourth and fifth thoracic segments separate. Abdomen con-

sisting of 5 segments, anal segment very small. Rostrum of moderate size with 2 filaments. Posterolateral margin of fifth thoracic segment with small, blunt corner. Antennule reaching third abdominal segment; segments 8 and 9, 10 and 12, and on right side 20 and 21 fused. Sensory structures on segments 2 and 3. Endopod of antenna little shorter than exopod. Basal segment of mandible palpus carrying 2 very small setae; exopod and endopod of about equal length. Mandible blade with 7 teeth and 1 strong seta. Two setae on second inner lobe of maxillule, 3 setae on third inner lobe, 4 setae on second basal segment, 3 setae on first, 2 setae on second, 3 setae on third endopodal segment, 7 setae on exopod. Maxilla stout, fifth lobe with coarse spine, endopod with 2 kinds of sensory filaments. Basal segments of maxilliped of nearly equal length, in endopod second segment longest. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs as well as exopods of first to fourth legs 3-segmented. Posterior sides of endopods and exopods of second to fourth legs beset with spines, very thickset in the fourth leg. Endopod of left fourth leg devoid of spinules. Fifth legs very asymmetrical. Left side 5-segmented, extremely long, exceeding half the total length of animal; first 4 segments slender, terminal segment short, bearing several setae. Right side 3-segmented, small, slightly longer than first segment of left side. Endopods absent. Total lengths (9 males) 2.56–2.84 mm. Allotype No. 125140.

Remarks. The female of *Xanthocalanus elongatus* shows some relationship to *X. echinatus* Sars, but is easily distinguished from it, as well as from all other species in the genus, by the heavy spinulation of the fourth leg and the structure of the fifth leg. The male differs from all other known males of *Xanthocalanus* by the enormous length of its left fifth leg.

The name *elongatus* alludes to the shape of the left fifth leg of the male.

Xanthocalanus macrocephalon n. sp.
Pl. VI, figs. 111–116; Pl. VII, figs. 117–127

Material examined: 4 females

Diagnosis. (female.) Head and first thoracic segment fused, separation indicated laterally by short line. Fourth and fifth thoracic segments incompletely separated. Abdomen 4-segmented. Rostrum small without filaments. Posterolateral margin of fifth thoracic segment angular. Antennule reaching end of cephalothorax, segments 8 and 9 fused. Exopod of antenna twice the length of endopod. Basal segment of mandible palpus with 3 setae; conspicuous hump on external side of mandible blade; teeth on chewing edge small. First inner lobe of maxillule bearing 10 spines, second and third inner lobes and second basal segment each with 2 setae, 2 and 5 setae on endopod, 4 setae on exopod. In maxilla first lobe with 4 setae, second to fourth lobes each with 3 setae, fifth lobe with 3 setae, 1 small spine and 1 sensory appendage, endopod with 2 types of sensory appendages. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented; exopods of all four legs 3-segmented. In second to fourth legs posterior sides of endopods armed with spinules, in fourth leg also basipod and exopod. Fifth leg 3-segmented, on posterior side, mainly externally, covered with small spines. Terminal segment with 1 small external spine, 1 long internal spine and 2 terminal points, not articulating with the segment. Total lengths 1.06–1.12 mm. Holotype No. 125141.

The male is unknown.

Remarks. Xanthocalanus macrocephalon is similar to *X. paraincertus* Grice and Hülsemann. *X. macrocephalon* can be distinguished from the latter mainly by its more slender body in lateral view, the absence of rostral filaments, the angular fifth thoracic segment, and the shorter spines on the exopod of the first leg. In *X. paraincertus* there are long rostral fila-

ments, the posterolateral margin of the fifth thoracic segment is rounded, and the spines of the exopod of the first leg are very long and curved.

The name *macrocephalon* refers to the relatively wide anterior portion of the head as seen in lateral view.

Amallophora macilenta n. sp.
Pl. VII, figs. 128–141; Pl. VIII, figs. 142–149

Material examined: 3 males

Diagnosis (male). Cephalothorax elongate. Head separated from first thoracic segment by fine line, dorsally extending posteriad close to anterior margin of second thoracic segment. Fourth and fifth thoracic segments fused. Abdomen 5-segmented. Rostrum of moderate size with 2 rostral filaments. Posterolateral margin of fifth thoracic segment rectangular with rounded corner. Second abdominal segment largest, about as wide as long; anal segment very short; second to fourth abdominal segments covered with slitlike pores. Antennule reaching posterior end of third abdominal segment. In right antennule segments 8–14 and 20 and 21 fused, on left side segments 7–14 fused and 20 and 21 incompletely separate. Exopod of antenna 1.5 times as long as endopod. Basal segment of mandibular palpus broad, carrying 2 slender setae. Teeth on mandible blade simple, on posterior side short, on anterior side longer. Spines on first inner lobe of maxillule modified; 2 setae on second inner lobe, 4 setae on third inner lobe, 5 setae on second basal segment, 2 and 6 setae on endopod, 10 setae on exopod. Maxilla small; 1 large amalla on endopod and 5 slender sensory appendages. Second basipodal segment of maxilliped slender, longer than first basipodal segment; second segment of endopod longest. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented. Exopods of first to fourth legs 3-segmented. Posterior sides of endopods of second to fourth legs armed with spines and spinules. Fifth legs slender; left side stronger than right, rudimentary endopods 1-segmented; first and second expodal segments of right fifth leg separated by fine line and equipped with minute spines; terminal spine on third segment long and slender. Distal end of second exopodal segment of left fifth leg with 4 or 5 setae, third segment with several horizontal rows of short hair and several terminal spines. Total lengths 5.16–5.41 mm. Holotype No. 125142.

The female is unknown.

Remarks. Amallophora macilenta is similar to *A. oculata* Tanaka, but differs mainly in its larger size, the absence of a lense below the rostrum, its rounded forehead (in lateral view), and in the nearly rectangular posterolateral margin of the fifth thoracic segment. *A. oculata* measures 3.40 mm, has a lense below the rostrum, a hollowed forehead near the base of the rostrum, and a narrowly rounded posterolateral margin on the fifth thoracic segment.

The name *macilenta* makes reference to the relatively slender body of this species.

Amallophora rotunda n. sp.
Pl. VIII, figs. 150–165; Pl. IX, figs. 166–171

Material examined: 3 males

Diagnosis (male). Head and first thoracic segment and fourth and fifth thoracic segments separate. Abdomen 5-segmented. Rostrum bifurcate with 2 filaments of moderate length. Posterolateral margin rounded ventrally and rather straight posteriorly. Antennule overreaching end of furca by about last 3 segments, segments 8 and 9 fused on both sides, incompletely fused with segment 10, segments 20 and 21 partly fused. Endopod of antenna about two-thirds the length of exopod. Basal segment of mandible palpus with 2 setae, mandible blade very small, edge with 5 teeth and 1 seta. Spines on first inner lobe of maxillule modified, 2 setae on second inner lobe, 4 setae on third inner lobe, 5 setae on second basal segment, 2, 2, and 4 setae on endopod, 10 setae on exopod.

Five lobes on maxilla relatively small, endopod carrying 1 large amalla. First basipodal segment of maxilliped with prominent hump proximally on anterior edge, segment widest distally, second basipodal segment widest proximally. Second segment of endopod longest. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs as well as exopods of first to fourth legs 3-segmented. Posterior sides of endopods of second to fourth legs and second exopodal segment of fourth leg with spinules. First basipodal segment of third leg with row of spinules, of fourth leg with row and patch of spinules. Fifth legs asymmetrical, both sides uniramous, 5-segmented. Left leg about 3 times as long as right leg. Third segment of right fifth leg with 1 small outer spine, distal segment with 2 small terminal spines. Third segment of left fifth leg with 1 small outer spine, distal end of fourth segment with fan of setae, terminal segment bearing some short hair on inner side and a patch of hair on the distal end. Total lengths 3.04–3.28 mm. Holotype No. 125143.

The female is unknown.

Remarks. Amallophora rotunda is closely related to *A. typica* A. Scott. It can, however, be distinguished by its slightly larger size, the less protruded fifth thoracic segment, the relatively shorter right fifth leg, and differences in the distal portion of the left fifth leg.

The name *rotunda* alludes to the body shape of this copepod, which is fuller than in the preceding species.

FAMILY DIAIXIDAE

Diaixis asymmetrica n. sp.

Pl. IX, figs. 172–190

Material examined: 1 female

Diagnosis (female). Head and first thoracic segment separate, fourth and fifth thoracic segments separate. Abdomen 4-segmented, anal segment very small. Rostrum divided, without filaments. Posterolateral corners of cephalothorax asymmetrical, left side pointed, right side lobate. Genital segment with two protrusions dorsally and one protrusion ventrally. Second abdominal segment with cuticular elevations ventrally and laterally. Antennules reaching to fourth thoracic segment; 24-segmented, segments 8 and 9 fused. Segment 1 through 21 with 1 or more rows of small spines. Antenna with endopod less than one-half of length of exopod. Basal segment of mandible palpus with 2 setae, blade elongate and bearing 4 rounded teeth and 2 slender setaelike structures. Maxillule with exopod bearing 2 sensory and 4 normal setae. Setae on first inner lobe very fine and elongate. Distal end of maxilla with 3 bulbous and 6 wormlike sensory setae. Basal segment of maxilliped bearing 4 sensory setae. Leg 1 with 3 exopodal segments each bearing 1 spine. Endopod 1-segmented. Rami of legs 2–4 elongate and bearing numerous small spines on anterior and posterior surfaces as well as on basal segments. First basal segment of fourth leg bearing proximally one large spine on right side and 2 smaller spines on left side. Total length 1.22 mm. Holotype No. 125144.

The male is unknown.

Remarks. This species differs from *Diaixis hibernica* (A. Scott) and *D. pygmaea* (T. Scott), the other two species in the genus, by 1) the lobate shape of the right posterolateral corner of the cephalothorax, 2) the numerous spines on the surface of the antennules and swimming legs, and 3) the presence of several large spines on the first basal segments of the fourth legs. The presence of two sensory setae on the exopod of the maxillule is also a distinctive characteristic of this species, and one which we have not observed in truly pelagic species.

FAMILY THARYBIDAE

Parundinella emarginata n. sp.

Pl. X, figs. 191–210

Material examined: 2 males

Diagnosis (male). Head and first tho-

racic segment fused, fourth and fifth thoracic segments partially fused. Abdomen 5-segmented, anal segment small. Rostrum bifurcate, each side bearing a filament. Posterolateral corners of cephalothorax symmetrical and emarginate. Antennules asymmetrical and broken distally in both specimens. Right antennule with segments 8–10 fused and apparently segments 21 and 22 fused. Left antennule with segments 8–10 only fused. Numerous aesthetasks proximally. Endopod of antenna approximately one-half length of exopod. Mandible palpus large, blade elongate and bearing 4 large teeth, several needlelike spines and a seta. Maxillule with 10 spines on first inner lobe, 3 setae on second inner lobe, 4 setae on third inner lobe, 4 setae on second basal segment, 7 setae on endopod, 7 setae on exopod, and 7 setae on first outer lobe. Distal end of maxilla bearing 3 bulbous and several wormlike sensory setae. Maxilliped with sensory setae on first basal segment. First leg with 3-segmented exopod and 1-segmented endopod. Second leg with 3-segmented exopod and 2-segmented endopod. Third and fourth legs with 3-segmented exopods and endopods. Numerous spines on endopod of third leg and basal segments and rami of fourth leg. Fifth legs biramous, reaching to end of furca. Right exopod 1-segmented, endopod fused with basal segment. Left exopod 3-segmented, proximal segment with large rounded protuberance. Left endopod elongate and 1-segmented. Total lengths .84 mm and .86 mm. Holotype No. 125145.

The female is unknown.

Remarks. The genus *Parundinella* was established by Fleminger (1957) to accommodate two species, *P. spinodenticula* and *P. manicula*, that he found in the Gulf of Mexico. The male of the latter species is not known. The segmentation of the fifth feet and the rounded posterolateral corner of the cephalothorax of *P. spinodenticula* are quite different from those in *P. emarginata*. Although the distal end of the right antennule of *P. emarginata* is broken off at segment 21, it appears that segments 21 and 22 are fused rather than segments 20 and 21 as in *P. spinodenticula*. *P. emarginata* could be the undescribed male of *P. manicula*. Since no females of *P. manicula* were found and since the species is known only from the Gulf of Mexico, we are not referring our specimens to this species.

The specific name *emarginata* refers to the shape of the posterolateral margin of the fifth thoracic segment.

Undinella altera n. sp.

Pl. X, figs. 211–214; Pl. XI, figs. 215–227

Material examined: 1 male

Diagnosis (male). Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Abdomen 5-segmented, anal segment very small. Rostrum absent. Posterolateral corner of thorax truncate. Right antennule consists of 22 free segments, segments 8–10, 20–21 fused. Left antennule consists of 23 segments, segments 8–10 fused. Aesthetasks numerous proximally on both antennules. Endopod of antenna approximately one-half the length of exopod. Mandible blade robust, cutting edge with coarse teeth and needlelike spines. Exopod of mandible smaller than endopod, basal segment bearing 2 coarse and 1 fine setae. First inner lobe of maxillule large, 2 and 5 setae on second and third inner lobes, respectively, 3 setae on second basal segment, 6 setae on endopod, 2 setae on exopod, and 7 setae on first outer lobe. Maxilla with 5 lobes arising distally. Second segment of maxilliped somewhat swollen. Exopods of first to fourth legs 3-segmented, endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented. Scattered spines on distal exodopal and endopodal segments of legs 2 and 3. Right fifth leg uniramous, 2-segmented. Proximal segment twice the length of distal segment. Endopod of left fifth leg elongate, reaching beyond end of right leg.

Exopod 3-segmented, distal segment with conspicuous lamella. Total length 1.60 mm. Holotype No. 125146.

The female is unknown.

Remarks. The males of *Undinella* are distinguished by the shape of the posterolateral corners of the cephalothorax and the structure of the fifth legs. In lateral view, the posterior end of the cephalothorax is truncate in *U. altera.* It is rounded, angular, or pointed in the other species. A distinct lamella is present on the distal segment of the exopod of the left fifth leg only in *U. compacta* and *U. altera.* In *U. compacta* the distal end of the first endopodal segment of the right leg reaches to the distal end of the exopod of the left leg. In *U. altera,* the distal end of the first endopodal segment reaches to about the mid point of the exopod.

The name *altera* should merely express that the described species is another species.

Undinella compacta n. sp.
Pl. XII, figs. 228–241; Pl. XIII, figs. 242–257

Material examined: 17 females, 40 males

Diagnosis (female). Anterior portion of head in dorsal view smoothly ovate, separated dorsally from first thoracic segment by fine line. Fourth and fifth thoracic segments fused. Abdomen 4-segmented. Rostrum or filaments absent. Posterolateral margin of fifth thoracic segment rounded with shallow indentation. Antennules not quite reaching end of cephalothorax, with 24 free segments, segments 8 and 9 fused, incompletely separated from segment 10. Exopod of antenna two times the length of endopod. Basal segment of mandible palpus with 2 coarse and 1 long slender setae; endopod longer than exopod. Mandible blade with about 7 monocuspidate teeth and 1 thick seta. Twelve spines on first inner lobe of maxillule, 3 setae on second inner lobe, 4 setae on third inner lobe, 3 setae on second basal segment, 2 and 5 setae on endopod, 3 setae on exopod. Lobes and endopod of maxilla located in distal half of appendage. Second basal segment of maxilliped about as long as first, thickened in proximal half. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs and exopods of first to fourth legs 3-segmented. Posterior sides of second to fourth legs with few spinules. Fifth leg 3-segmented; distal segment slender with 1 coarse terminal spine and 1 terminal spinelike point; distal segment, measured to the insertion of the spine, 1.5 times the length of preceding segment. Total lengths 1.16–1.28 mm. Holotype No. 125147.

Diagnosis (male). Anterior portion of head in dorsal view truncate, separated dorsally from first thoracic segment by fine line. Fourth and fifth thoracic segments fused. Abdomen consisting of 5 segments, anal segment very short. Rostrum or filaments absent. Posterolateral margin of fifth thoracic segment angular with rounded tip. Antennules reaching posterior end of second abdominal segment; segments 8–10 and 20 and 21 fused in right antennule, segments 8–10 only fused in left antennule. Sensory appendages on segments 2, 3, 5, 7, 9. Other head appendages and swimming legs as in the female. Fifth leg large, exceeding end of furca. In right fifth leg second and third exopodal segments fused to one slender segment bearing a hump posteriorly in the distal half, terminal segment flattened; endopod lacking. In left fifth leg basipod large; endopod 1-segmented, about twice as long as 3-segmented exopod; terminal segment of exopod slender, with lamella reinforced by "veins," especially at the tip. Total lengths 1.00–1.22 mm. Allotype No. 125148.

Remarks. Undinella compacta approaches the genus *Tharybis* in the relatively large first inner lobe of the maxillule, the swollen second basipodal segment of the maxilliped, and the elongate terminal segment of the fifth leg. However, the present species is placed in the genus *Undinella* because the head and first thoracic segment and

racic segment fused, fourth and fifth thoracic segments partially fused. Abdomen 5-segmented, anal segment small. Rostrum bifurcate, each side bearing a filament. Posterolateral corners of cephalothorax symmetrical and emarginate. Antennules asymmetrical and broken distally in both specimens. Right antennule with segments 8–10 fused and apparently segments 21 and 22 fused. Left antennule with segments 8–10 only fused. Numerous aesthetasks proximally. Endopod of antenna approximately one-half length of exopod. Mandible palpus large, blade elongate and bearing 4 large teeth, several needlelike spines and a seta. Maxillule with 10 spines on first inner lobe, 3 setae on second inner lobe, 4 setae on third inner lobe, 4 setae on second basal segment, 7 setae on endopod, 7 setae on exopod, and 7 setae on first outer lobe. Distal end of maxilla bearing 3 bulbous and several wormlike sensory setae. Maxilliped with sensory setae on first basal segment. First leg with 3-segmented exopod and 1-segmented endopod. Second leg with 3-segmented exopod and 2-segmented endopod. Third and fourth legs with 3-segmented exopods and endopods. Numerous spines on endopod of third leg and basal segments and rami of fourth leg. Fifth legs biramous, reaching to end of furca. Right exopod 1-segmented, endopod fused with basal segment. Left exopod 3-segmented, proximal segment with large rounded protuberance. Left endopod elongate and 1-segmented. Total lengths .84 mm and .86 mm. Holotype No. 125145.

The female is unknown.

Remarks. The genus *Parundinella* was established by Fleminger (1957) to accommodate two species, *P. spinodenticula* and *P. manicula*, that he found in the Gulf of Mexico. The male of the latter species is not known. The segmentation of the fifth feet and the rounded posterolateral corner of the cephalothorax of *P. spinodenticula* are quite different from those in *P. emarginata*. Although the distal end of the right antennule of *P. emarginata* is broken off at segment 21, it appears that segments 21 and 22 are fused rather than segments 20 and 21 as in *P. spinodenticula*. *P. emarginata* could be the undescribed male of *P. manicula*. Since no females of *P. manicula* were found and since the species is known only from the Gulf of Mexico, we are not referring our specimens to this species.

The specific name *emarginata* refers to the shape of the posterolateral margin of the fifth thoracic segment.

Undinella altera n. sp.

Pl. X, figs. 211–214; Pl. XI, figs. 215–227

Material examined: 1 male

Diagnosis (male). Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Abdomen 5-segmented, anal segment very small. Rostrum absent. Posterolateral corner of thorax truncate. Right antennule consists of 22 free segments, segments 8–10, 20–21 fused. Left antennule consists of 23 segments, segments 8–10 fused. Aesthetasks numerous proximally on both antennules. Endopod of antenna approximately one-half the length of exopod. Mandible blade robust, cutting edge with coarse teeth and needlelike spines. Exopod of mandible smaller than endopod, basal segment bearing 2 coarse and 1 fine setae. First inner lobe of maxillule large, 2 and 5 setae on second and third inner lobes, respectively, 3 setae on second basal segment, 6 setae on endopod, 2 setae on exopod, and 7 setae on first outer lobe. Maxilla with 5 lobes arising distally. Second segment of maxilliped somewhat swollen. Exopods of first to fourth legs 3-segmented, endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented. Scattered spines on distal exodopal and endopodal segments of legs 2 and 3. Right fifth leg uniramous, 2-segmented. Proximal segment twice the length of distal segment. Endopod of left fifth leg elongate, reaching beyond end of right leg.

Exopod 3-segmented, distal segment with conspicuous lamella. Total length 1.60 mm. Holotype No. 125146.

The female is unknown.

Remarks. The males of *Undinella* are distinguished by the shape of the posterolateral corners of the cephalothorax and the structure of the fifth legs. In lateral view, the posterior end of the cephalothorax is truncate in *U. altera.* It is rounded, angular, or pointed in the other species. A distinct lamella is present on the distal segment of the exopod of the left fifth leg only in *U. compacta* and *U. altera.* In *U. compacta* the distal end of the first endopodal segment of the right leg reaches to the distal end of the exopod of the left leg. In *U. altera,* the distal end of the first endopodal segment reaches to about the mid point of the exopod.

The name *altera* should merely express that the described species is another species.

Undinella compacta n. sp.
Pl. XII, figs. 228–241; Pl. XIII, figs. 242–257

Material examined: 17 females, 40 males

Diagnosis (female). Anterior portion of head in dorsal view smoothly ovate, separated dorsally from first thoracic segment by fine line. Fourth and fifth thoracic segments fused. Abdomen 4-segmented. Rostrum or filaments absent. Posterolateral margin of fifth thoracic segment rounded with shallow indentation. Antennules not quite reaching end of cephalothorax, with 24 free segments, segments 8 and 9 fused, incompletely separated from segment 10. Exopod of antenna two times the length of endopod. Basal segment of mandible palpus with 2 coarse and 1 long slender setae; endopod longer than exopod. Mandible blade with about 7 monocuspidate teeth and 1 thick seta. Twelve spines on first inner lobe of maxillule, 3 setae on second inner lobe, 4 setae on third inner lobe, 3 setae on second basal segment, 2 and 5 setae on endopod, 3 setae on exopod. Lobes and endopod of maxilla located in distal half of appendage. Second basal segment of maxilliped about as long as first, thickened in proximal half. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs and exopods of first to fourth legs 3-segmented. Posterior sides of second to fourth legs with few spinules. Fifth leg 3-segmented; distal segment slender with 1 coarse terminal spine and 1 terminal spinelike point; distal segment, measured to the insertion of the spine, 1.5 times the length of preceding segment. Total lengths 1.16–1.28 mm. Holotype No. 125147.

Diagnosis (male). Anterior portion of head in dorsal view truncate, separated dorsally from first thoracic segment by fine line. Fourth and fifth thoracic segments fused. Abdomen consisting of 5 segments, anal segment very short. Rostrum or filaments absent. Posterolateral margin of fifth thoracic segment angular with rounded tip. Antennules reaching posterior end of second abdominal segment; segments 8–10 and 20 and 21 fused in right antennule, segments 8–10 only fused in left antennule. Sensory appendages on segments 2, 3, 5, 7, 9. Other head appendages and swimming legs as in the female. Fifth leg large, exceeding end of furca. In right fifth leg second and third exopodal segments fused to one slender segment bearing a hump posteriorly in the distal half, terminal segment flattened; endopod lacking. In left fifth leg basipod large; endopod 1-segmented, about twice as long as 3-segmented exopod; terminal segment of exopod slender, with lamella reinforced by "veins," especially at the tip. Total lengths 1.00–1.22 mm. Allotype No. 125148.

Remarks. Undinella compacta approaches the genus *Tharybis* in the relatively large first inner lobe of the maxillule, the swollen second basipodal segment of the maxilliped, and the elongate terminal segment of the fifth leg. However, the present species is placed in the genus *Undinella* because the head and first thoracic segment and

fourth and fifth thoracic segments are partially separate, the exopod of the maxillule bears 3 setae, and the lobes of the maxilla are crowded within the distal half of the appendage. The absence of a rostrum and rostral filaments is unique in the family Tharybidae.

The female of *Undinella compacta* can be distinguished from the other species of the genus by the rounded posterolateral margin of the fifth thoracic segment and the shape and armature of the fifth leg. The male resembles *U. altera*, but it can be distinguished by the angular shape of the posterolateral margin of the fifth thoracic segment that is truncate in *altera* and by the longer fused second and third exopodal segments of the right fifth leg that reach to the distal end of the left exopod; in *altera* this segment is shorter.

The name *compacta* refers to the relatively stout body of this copepod.

Undinella hampsoni n. sp.

Pl. XIV, figs. 258–272; Pl. XV, figs. 273–285

Material examined: 11 females, 2 males

Diagnosis (female). Head and first thoracic segment partially separate, fourth and fifth thoracic segments partially separate. Abdomen 4-segmented, anal segment small. Rostrum bifurcate, each side bearing a slender filament. Posterolateral corners of cephalothorax asymmetrical. In dorsal view, right side with fingerlike protrusion, left side more evenly rounded. Genital segment with prominent bulge on dorsal side near posterior end. Antennules reaching to middle of abdomen, with 24 free segments, aesthetasks more numerous proximally. Exopod of antenna approximately twice the length of endopod. Exopod of mandible reduced, basal segment with 2 setae. Mandible blade with coarse cuspate and spiniform teeth. Maxillule with enlarged first inner lobe, 2 and 4 setae on second and third inner lobes respectively, 4 setae on second basal segment, 6 setae on endopod, 2 setae on exopod, and 6 setae on first outer lobe. Lobes on maxilla arise from distal end. Second segment of maxilliped elongate. Exopod of first leg 2-segmented, of second to fourth legs 3-segmented. Endopod of first leg 1-segmented, of second leg 2-segmented, of third and fourth legs 3-segmented. Fifth legs asymmetrical, right leg longer than left and reaching beyond genital segment. Terminal segment of right leg twice the length of the preceding segment. Distal segment of both legs each with 1 lateral and 3 terminal spines. Total lengths 1.90–2.12 mm. Holotype No. 125149.

Diagnosis (male). Head and first thoracic segment fused, fourth and fifth thoracic segments fused. Abdomen 5-segmented. Right first antennule consists of 22 free segments, segments 8–10, 20 and 21 fused. Left first antennule consists of 23 free segments, segments 8–10 fused. Rostrum, mouth appendages, and segmentation of first four pairs of legs as in female. Fifth legs asymmetrical, complex. Right leg uniramous, 2-segmented. Left exopod 3-segmented, terminal segment with group of setae. Distal protuberance of second segment provided with hair and a raised, rounded process. Total lengths 1.98–2.00 mm. Allotype No. 125150.

Remarks. The female of *U. hampsoni* is similar to *U. frontalis* (Tanaka) which was first described from a female specimen collected in Suruga Bay, Japan, and subsequently from specimens (female and male) obtained in the North Pacific (Brodsky, 1950) and in Sagami Bay, Japan (Tanaka, 1960). The two females of these species are best distinguished by the structure of the genital segment and fifth pair of legs. In *U. hampsoni* there is a marked bulge on the dorsal surface of the genital segment near the posterior end, and the distal segment of the right fifth leg is much longer than the penultimate segment. In *U. frontalis* there is no protuberance on the genital segment, and the two distal segments of the right fifth leg are subequal. The males of the two species are readily

distinguished by the structure and ornamentation of the protrusion of the second segment of the left exopod. In *U. hampsoni* this protrusion has a raised depression and is pubescent. In *U. frontalis* it is naked.

The species is named for Mr. George Hampson, Biology Department, Woods Hole Oceanographic Institution, who participated in the collection of the samples.

LITERATURE CITED

Brodsky, K. A. 1950. Calanoida of polar and far eastern seas of the U.S.S.R. Opredel. Fauna SSSR, Izd. Zool. Inst. Akad. Nauk SSSR, **35**: 1–442. (In Russian).

Farran, G. P. 1905. Report on the Copepoda of the Atlantic slope off Counties Mayo and Galway. Sci. Invest. Fish. Br. Ire., 1902–1903, pt. 2, app. 2: 23–52.

Fleminger, A. 1957. New genus and two new species of Tharybidae (Copepoda Calanoida) from the Gulf of Mexico with remarks on the status of the family. U. S. Fish & Wildlife Serv., Fishery Bull. 116, **61**: 345–354.

Frolander, H. F., and I. Pratt. 1962. A bottom skimmer. Limnol. Oceanogr., 7(1): 104–106.

Hutchinson, G. E. 1967. A Treatise on Limnology. Vol. II. Introduction to Lake Biology and the Limnoplankton. New York: John Wiley and Sons, Inc. vii-xi + 1115 pp.

Matthews, J. B. L. 1964. On the biology of some bottom-living copepods (Aetideidae and Phaennidae) from western Norway. Sarsia **16**: 1–46.

Sars, G. O. 1902. An account of the Crustacea of Norway IV. Copepoda Calanoida pt. III & IV: 29–48, pt. V & VI: 49–72.

———. 1924–1925. Copépodes, particulièrement bathypélagiques provenant des Campagnes Scientifiques du Prince Albert I^{er} de Monaco. Résult. Camp. Sci. Monaco, vol. **68**, text (1925); atlas (1924).

Tanaka, O. 1960. The pelagic copepods of the Izu Region, Middle Japan; Systematic account VI: Families Phaennidae and Tharybidae. Publ. Seto Mar. Biol. Lab., **8**(1): 85–135.

Plate I

Aetideopsis magna n. sp., male

Figure 3. Dorsal
Figure 4. Lateral
Figure 5. Fourth and fifth thoracic segments and first abdominal segment, lateral
Figure 6. Anterior portion of head, lateral
Figure 7. Rostrum, ventral
Figure 8. Right antennule
Figure 9. Antenna
Figure 10. Mandible palpus
Figure 11. Maxillule
Figure 12. Maxilla
Figure 13. Maxilliped
Figure 14. First leg
Figure 15. Second leg, exopod broken short
Figure 16. Third leg, exopod and endopod broken short
Figure 17. Fourth leg, exopod broken short
Figure 18. Fifth legs
Figure 19. Tip of left fifth leg

Comantenna recurvata n. sp., female

Figure 20. Dorsal
Figure 21. Lateral
Figure 22. Antenna
Figure 23. Mandible palpus
Figure 24. Mandible blade

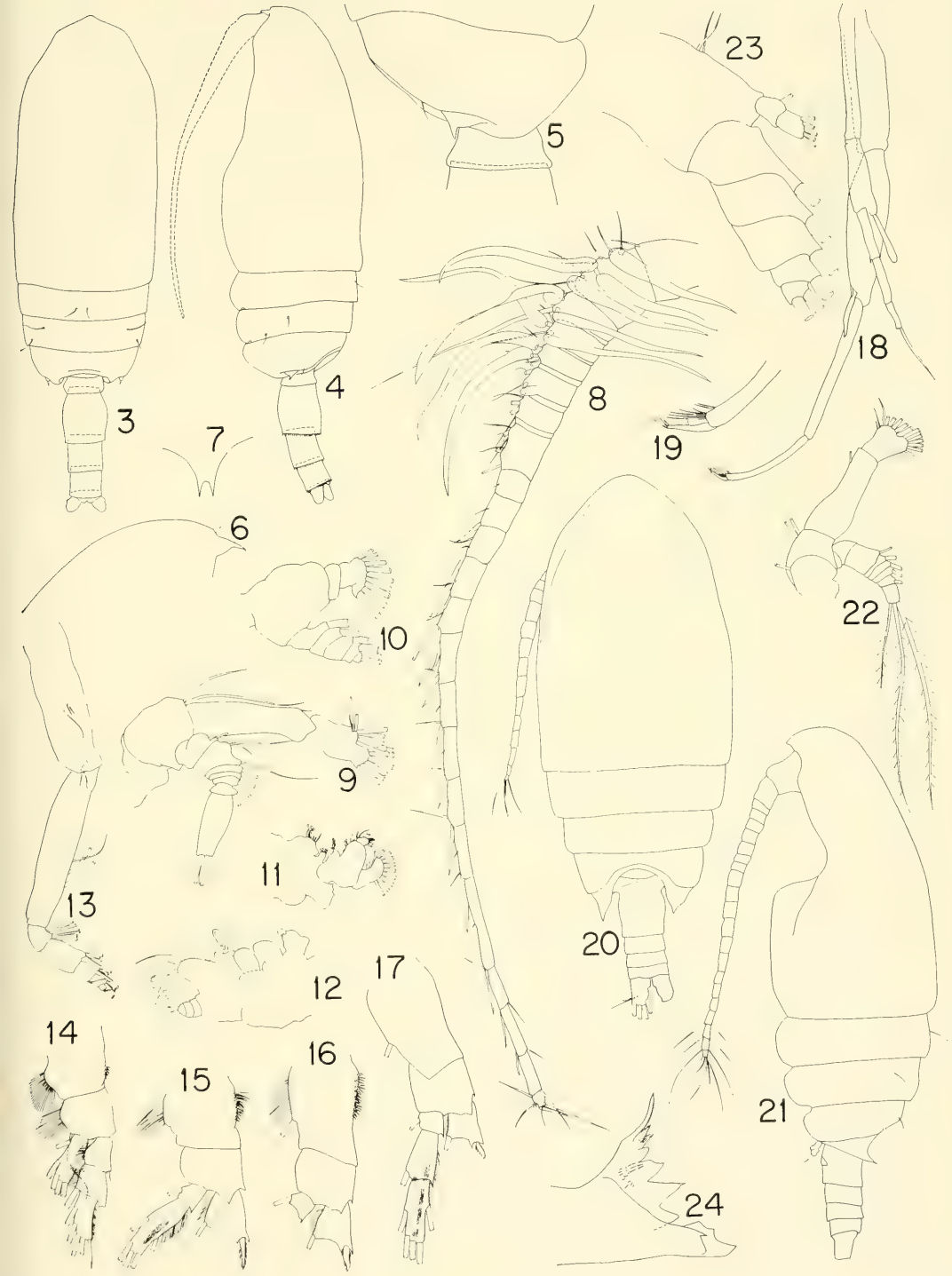
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Plate II

Comantenna recurvata n. sp., female (continued)

Figure 25. Antennule
Figure 26. Maxillule
Figure 27. Maxillule, third inner lobe
Figure 28. Maxilla
Figure 29. Maxilla, distal lobe, other side
Figure 30. Maxilliped
Figure 31. First leg
Figure 32. Second leg
Figure 33. Third leg
Figure 34. Fourth leg
Figure 35. Fifth legs

Xanthocalanus alvinae n. sp., female

Figure 36. Fourth and fifth thoracic segments and abdomen, lateral
Figure 37. Anterior portion of head, lateral
Figure 38. Fifth thoracic segment and abdomen, dorsal
Figure 39. Rostrum, ventral
Figure 40. Antenna

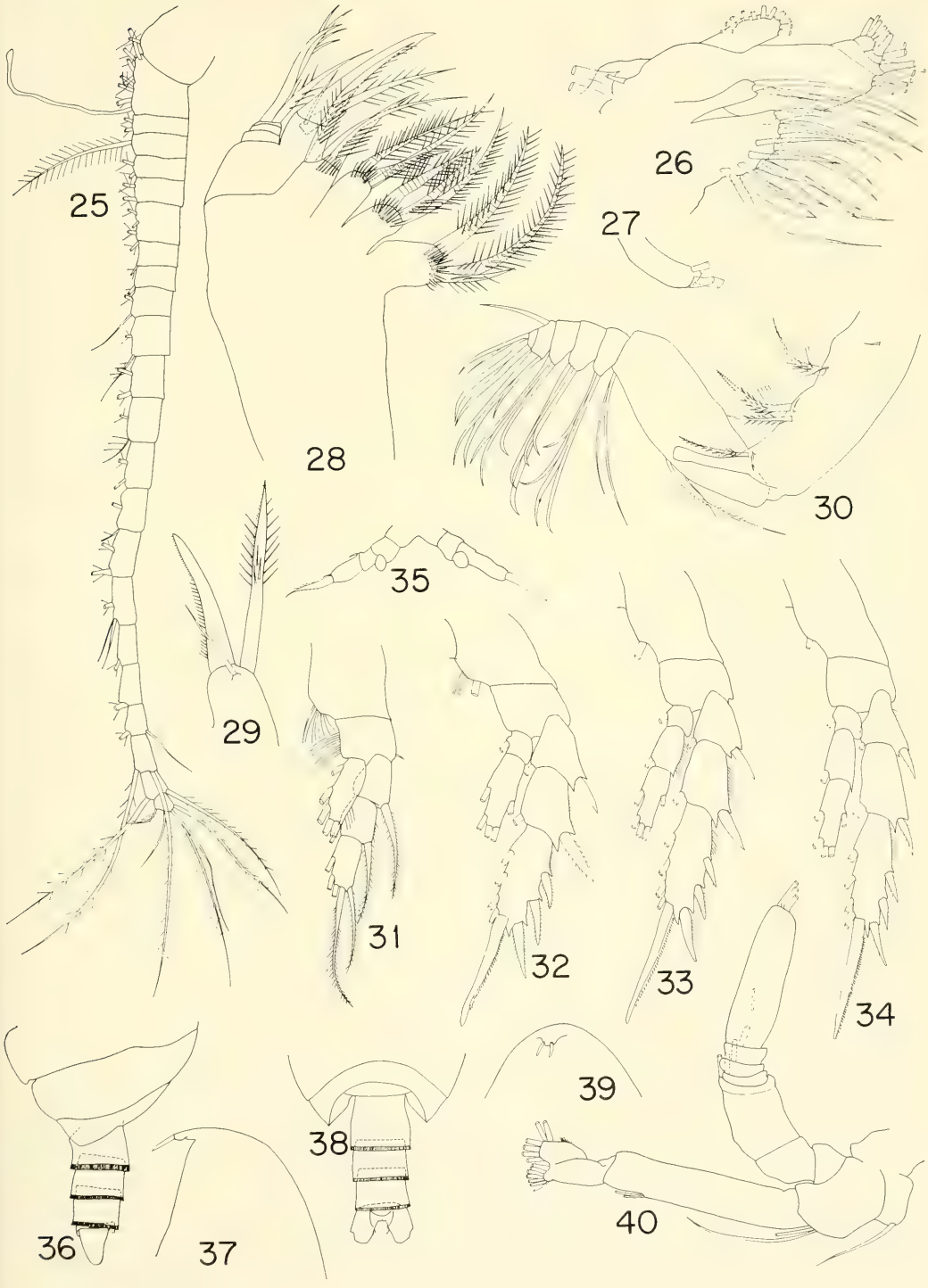
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Plate IV

Xanthocalanus distinctus n. sp., male (continued)

Figure 58. Anterior portion of head
Figure 59. Left antennule, lateral
Figure 60. Antenna
Figure 61. Mandible palpus
Figure 62. Mandible blade
Figure 63. Maxillule
Figure 64. Maxilla
Figure 65. Maxilliped
Figure 66. First leg
Figure 67. Second leg
Figure 68. Third leg
Figure 69. Terminal spine of third leg
Figure 70. Fourth leg
Figure 71. Fifth legs
Figure 72. Right fifth leg, posterior side
Figure 73. Tip of left fifth leg

Xanthocalanus elongatus n. sp., female

Figure 74. Lateral
Figure 75. Dorsal
Figure 76. Fifth thoracic segment and abdomen, lateral
Figure 77. Fifth thoracic segment and abdomen, dorsal
Figure 78. Fourth and fifth abdominal segments and furca, ventral

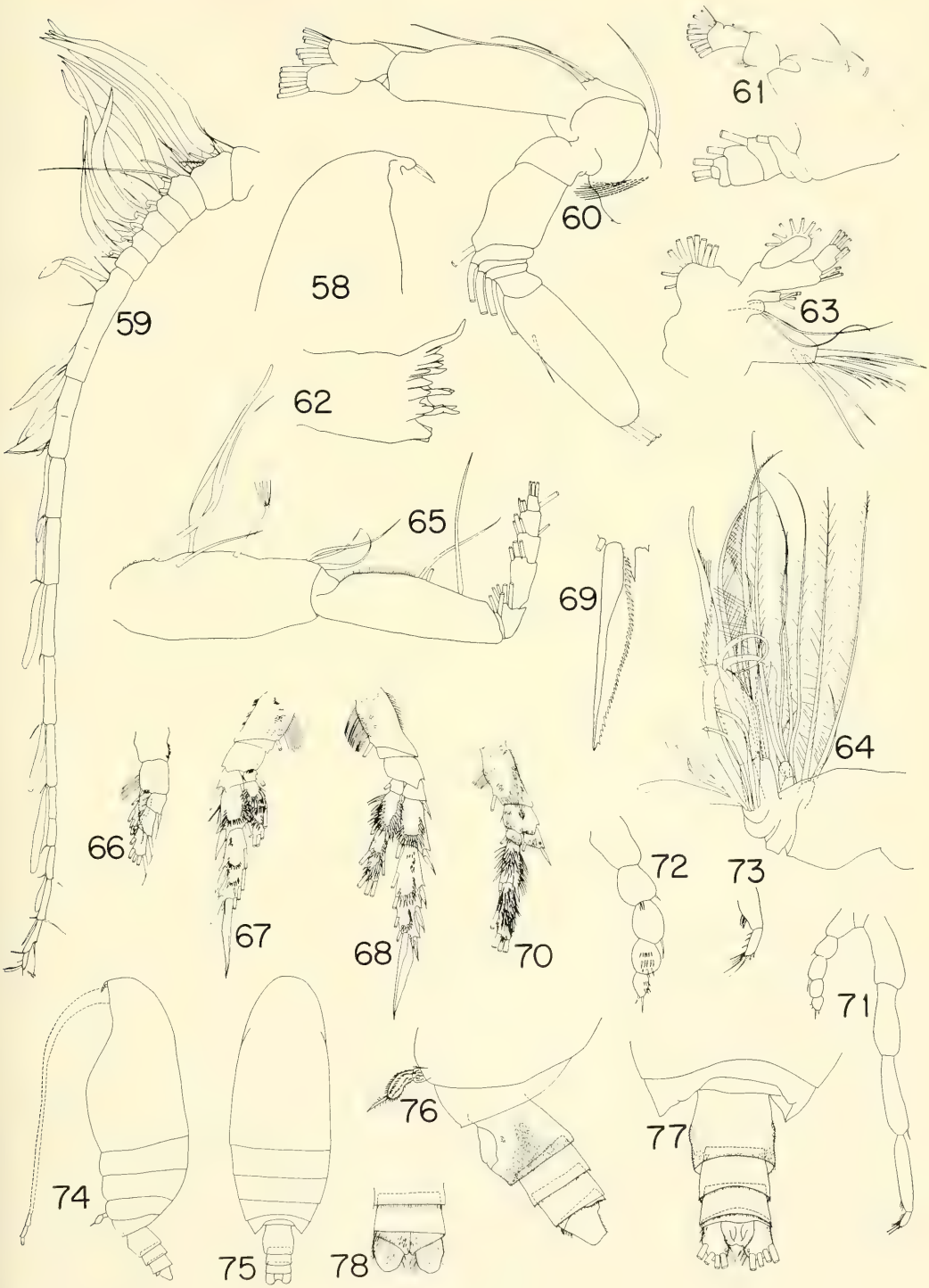
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Plate V

Xanthocalanus elongatus n. sp., female (continued)

Figure 79. Left antennule
Figure 80. Antenna
Figure 81. Mandible palpus
Figure 82. Mandible blade
Figure 83. Maxillule
Figure 84. Maxilla
Figure 85. Maxilliped
Figure 86. First leg
Figure 87. Second leg, terminal spine omitted
Figure 88. Third leg
Figure 89. External spine of second expodal segment of third leg
Figure 90. Fourth leg
Figure 91. Fifth leg

Xanthocalanus elongatus n. sp., male

Figure 92. Lateral
Figure 93. Dorsal
Figure 94. Anterior portion of head, lateral
Figure 95. Fourth and fifth thoracic segments and genital segment, lateral
Figure 96. Antenna

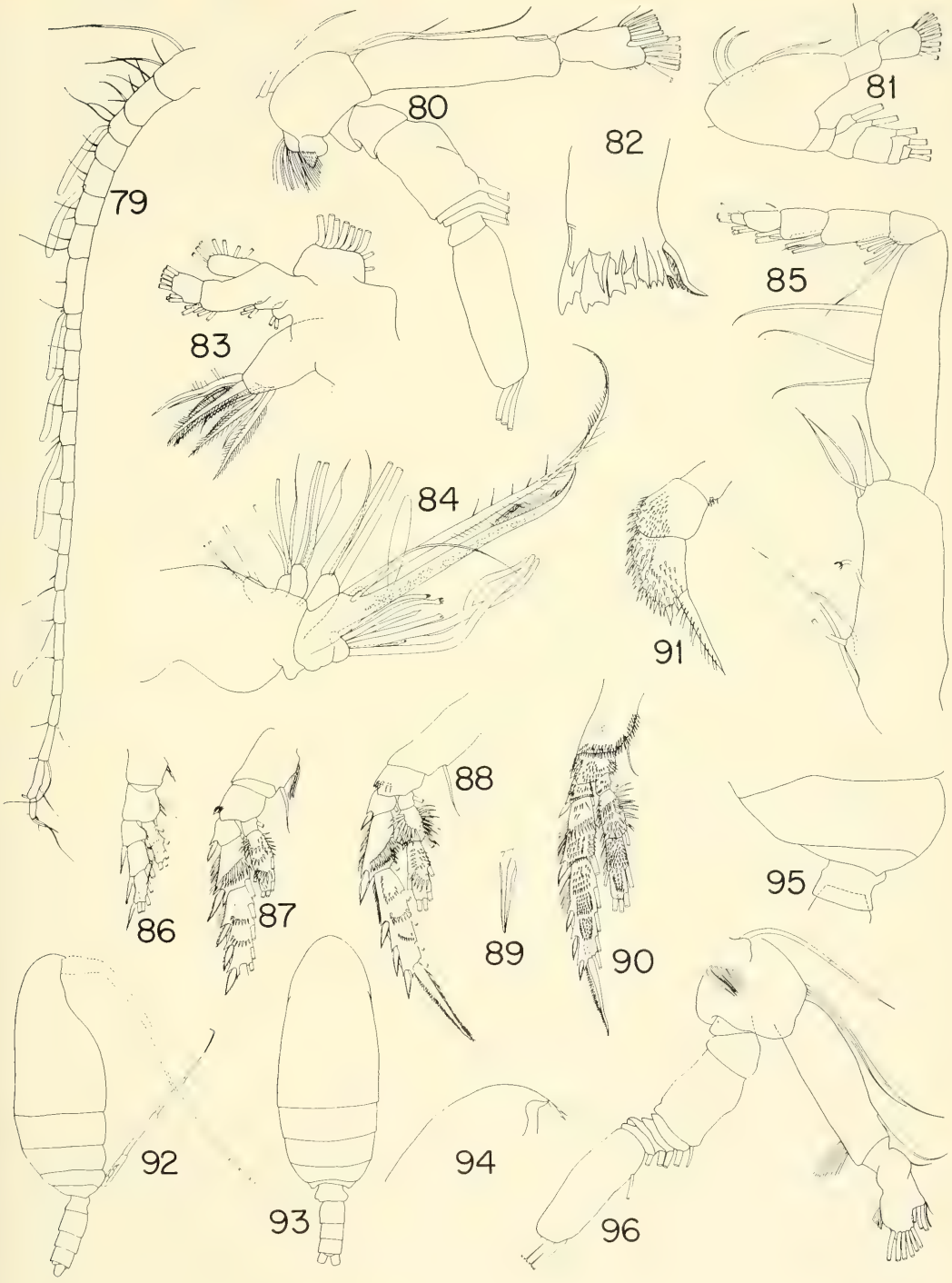
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Plate VI

Xanthocalanus elongatus n. sp., male (continued)

Figure 97. Right antennule
Figure 98. Mandible palpus
Figure 99. Mandible blade
Figure 100. Maxillule
Figure 101. Maxilla
Figure 102. Maxilliped
Figure 103. First leg
Figure 104. Second leg
Figure 105. Third leg
Figure 106. Fourth leg
Figure 107. Fifth legs
Figure 108. Right fifth leg and first segment of left fifth leg
Figure 109. Tip of left fifth leg, posterior side
Figure 110. Tip of right fifth leg, anterior side

Xanthocalanus macrocephalon n. sp., female

Figure 111. Lateral
Figure 112. Dorsal
Figure 113. Anterior portion of head, lateral
Figure 114. Anterior portion of head, ventral
Figure 115. Fifth thoracic segment and abdomen, lateral
Figure 116. Right antennule

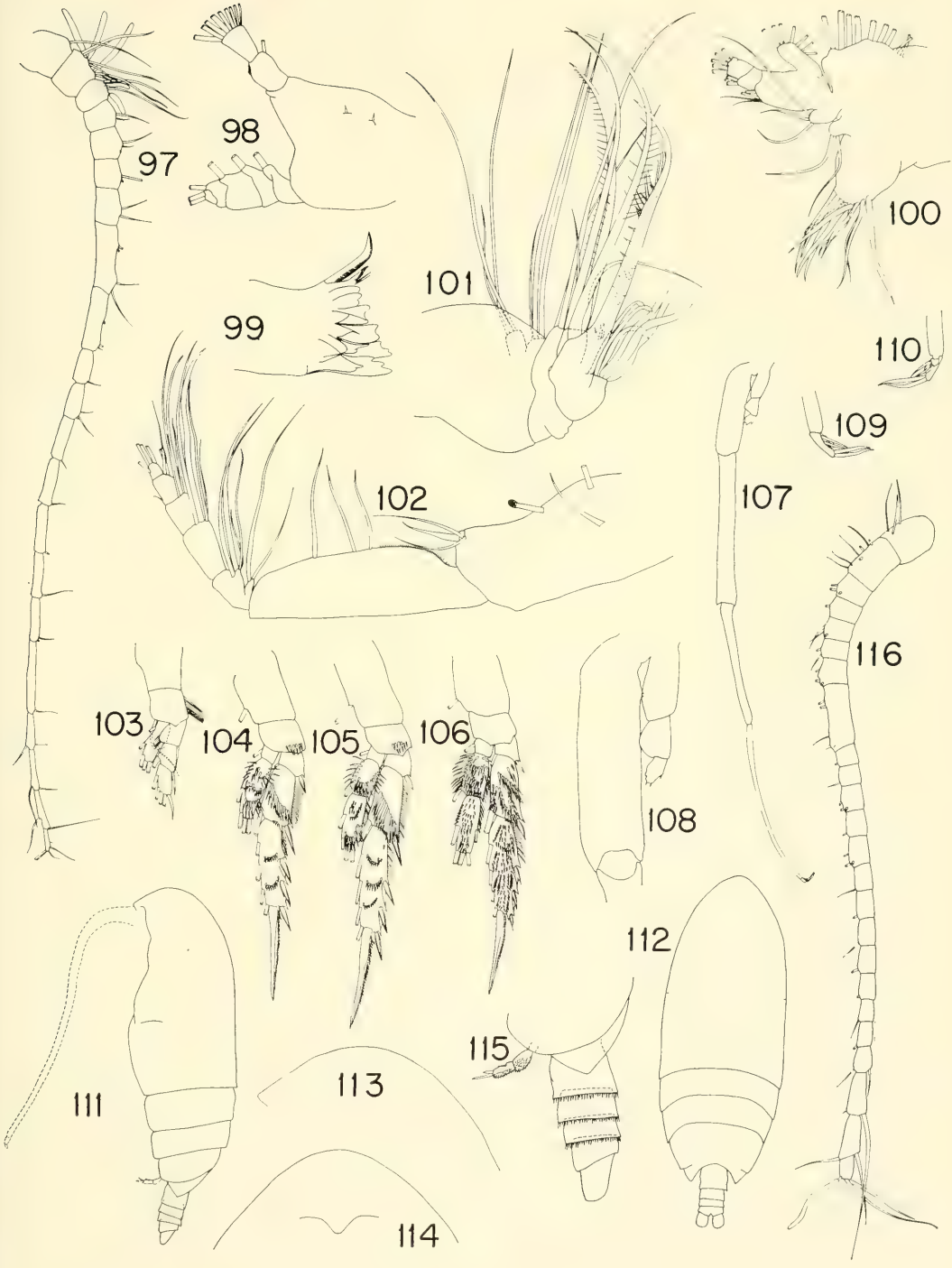
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Plate VII

Xanthocalanus macrocephalon n. sp., female (continued)

Figure 117. Antenna
Figure 118. Mandible palpus
Figure 119. Mandible blade
Figure 120. Maxillule
Figure 121. Maxilla
Figure 122. Maxilliped
Figure 123. First leg
Figure 124. Second leg
Figure 125. Third leg
Figure 126. Fourth leg
Figure 127. Fifth leg

Amallophora macilenta n. sp., male

Figure 128. Dorsal
Figure 129. Lateral
Figure 130. Rostrum
Figure 131. Portion of genital segment, enlarged
Figure 132. Right antennule
Figure 133. Exopod of antenna
Figure 134. Endopod and basipod of antenna
Figure 135. Mandible palpus
Figure 136. Mandible blade
Figure 137. Maxillule
Figure 138. Modified spine of first inner lobe of maxillule
Figure 139. Maxilla
Figure 140. Maxilla, other side
Figure 141. Maxilliped

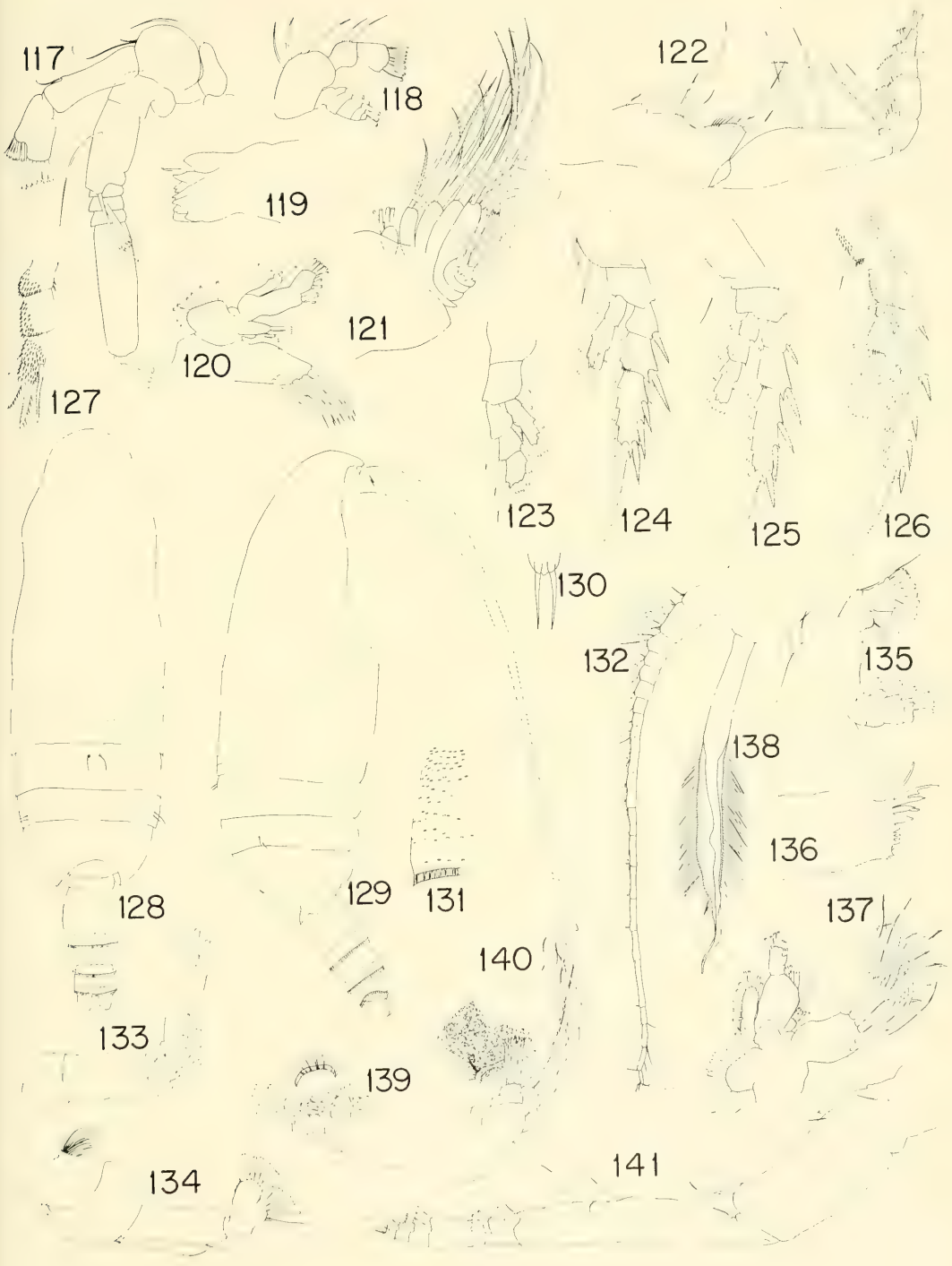
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Plate VIII

Amallophora macilenta n. sp., male (continued)

Figure 142. First leg
Figure 143. Second leg, exopod broken off
Figure 144. Third leg, exopod broken off
Figure 145. Fourth leg
Figure 146. Fifth legs
Figure 147. Endopod of left fifth leg
Figure 148. Tip of left fifth leg, posterior side
Figure 149. Tip of left fifth leg, anterior side

Amallophora rotunda n. sp., male

Figure 150. Lateral
Figure 151. Dorsal
Figure 152. Ventral margin of second and third thoracic segments
Figure 153. Anterior portion of head, lateral
Figure 154. Anterior portion of head, ventral
Figure 155. Right antennule
Figure 156. Antenna
Figure 157. Mandible palpus
Figure 158. Mandible blade
Figure 159. Maxillule
Figure 160. Modified spine of first inner lobe of maxillule
Figure 161. Maxilla
Figure 162. Maxilliped
Figure 163. Right maxilliped, slightly turned outward
Figure 164. First leg, posterior
Figure 165. Endopod of first leg, anterior

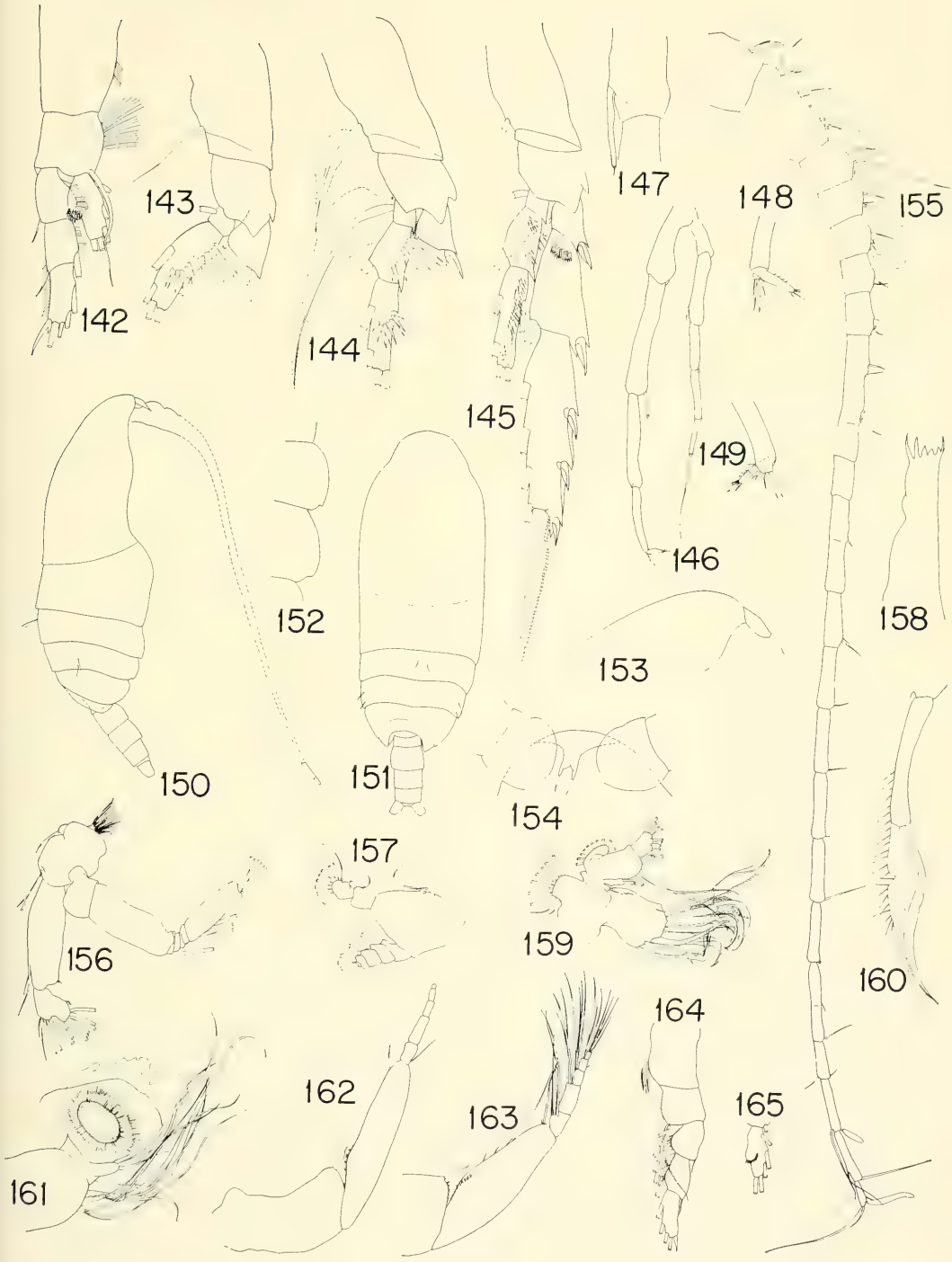
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Plate IX

Amallophora rotunda n. sp., male (continued)

Figure 166. Second leg
Figure 167. Third leg
Figure 168. Fourth leg
Figure 169. External spine of second exopodal segment of fourth leg
Figure 170. Fifth legs
Figure 171. Tip of left fifth leg, posterior side

Diaixis asymmetrica, n. sp., female

Figure 172. Lateral
Figure 173. Dorsal
Figure 174. Abdomen, ventral
Figure 175. Fourth and fifth thoracic segments and abdomen, left side
Figure 176. Fifth thoracic segment and genital segment, right side
Figure 177. Left antennule
Figure 178. Antenna
Figure 179. Mandible palpus
Figure 180. Mandible blade
Figure 181. Maxillule
Figure 182. Maxilla, only sensory setae shown
Figure 183. Maxilla, other side, sensory setae omitted
Figure 184. Maxilliped, setae on endopod omitted
Figure 185. Endopod of maxilliped
Figure 186. First leg
Figure 187. Second leg, exopod broken off
Figure 188. Left third leg, endopod broken off
Figure 189. Endopod of right third leg
Figure 190. Fourth legs, incomplete

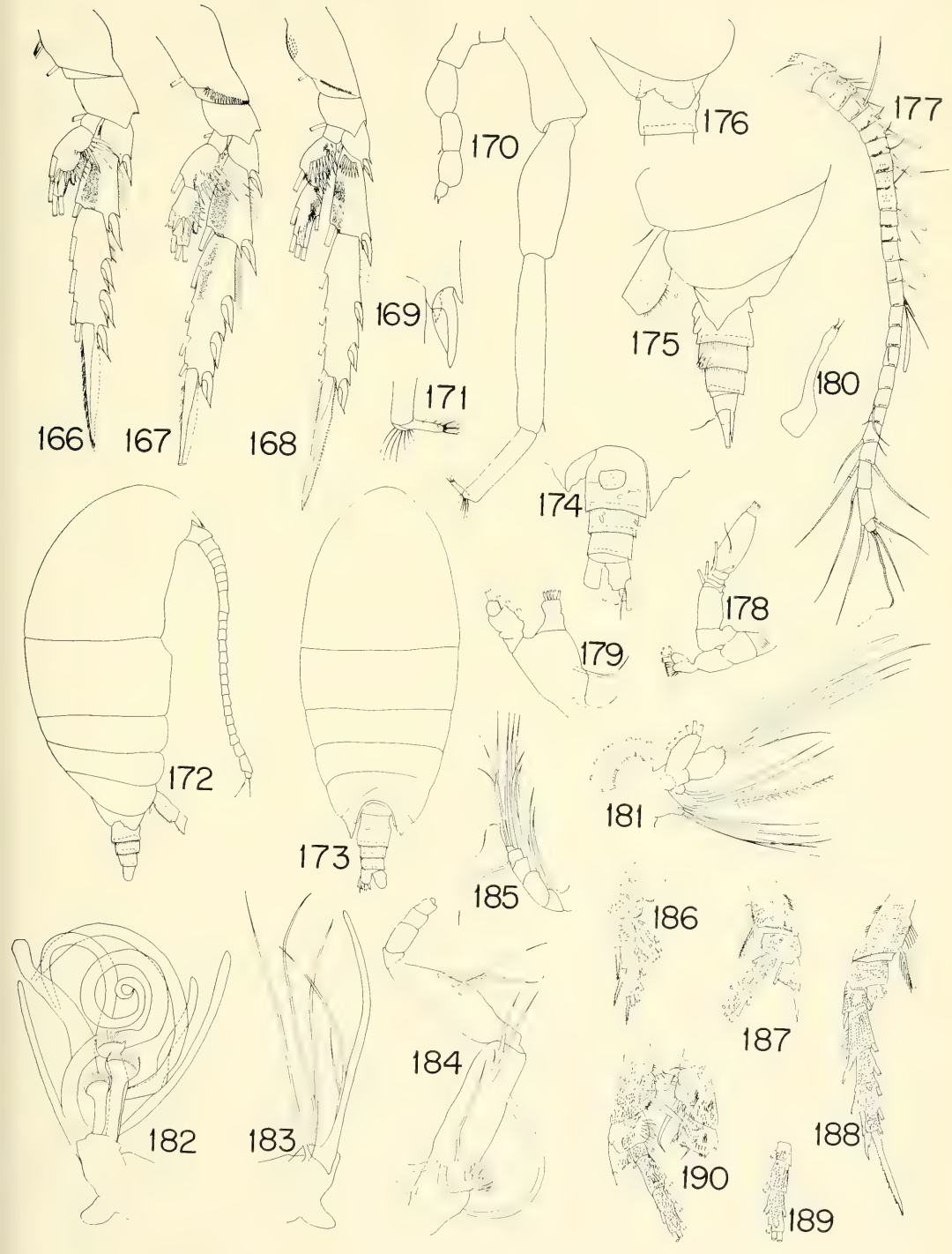
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Plate X

Parundinella emarginata n. sp., female

Figure 191. Dorsal
Figure 192. Lateral
Figure 193. Fifth thoracic segment and genital segment, dorsal
Figure 194. Fifth thoracic segment, abdomen and fifth leg, right side
Figure 195. Fifth thoracic segment, abdomen and fifth leg, left side
Figure 196. Rostrum
Figure 197. Right antennule, broken short
Figure 198. Antenna
Figure 199. Mandible palpus
Figure 200. Mandible blade
Figure 201. Maxillule
Figure 202. Maxilla
Figure 203. Maxilliped
Figure 204. First leg
Figure 205. Second leg
Figure 206. Third leg
Figure 207. Fourth leg
Figure 208. Fifth legs, anterior side
Figure 209. Fifth legs, posterior side
Figure 210. Left fifth leg, second and third segments of exopod

Undinella altera n. sp., male

Figure 211. Antenna
Figure 212. Fourth and fifth thoracic segments and genital segment
Figure 213. Mandible
Figure 214. Maxillule

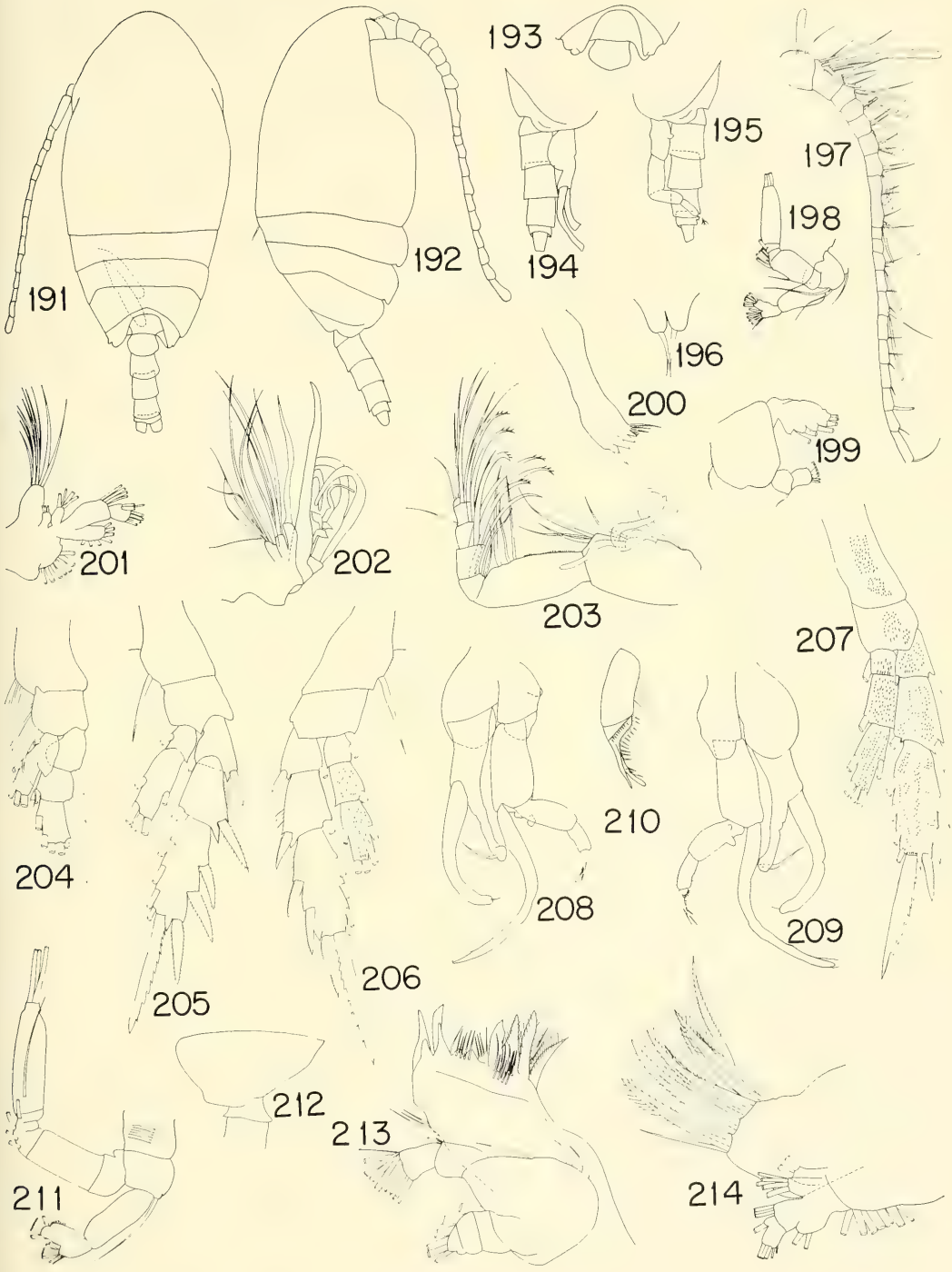
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Plate XI

Undinella altera n. sp., male (continued)

Figure 215. Dorsal
Figure 216. Lateral
Figure 217. Left antennule
Figure 218. Maxilla
Figure 219. Maxilliped
Figure 220. First leg
Figure 221. Second leg
Figure 222. Terminal spine of second leg
Figure 223. Third leg
Figure 224. Fourth leg
Figure 225. Fifth legs, anterior side
Figure 226. Distal portion of fifth legs, posterior side
Figure 227. Exopod of left fifth leg

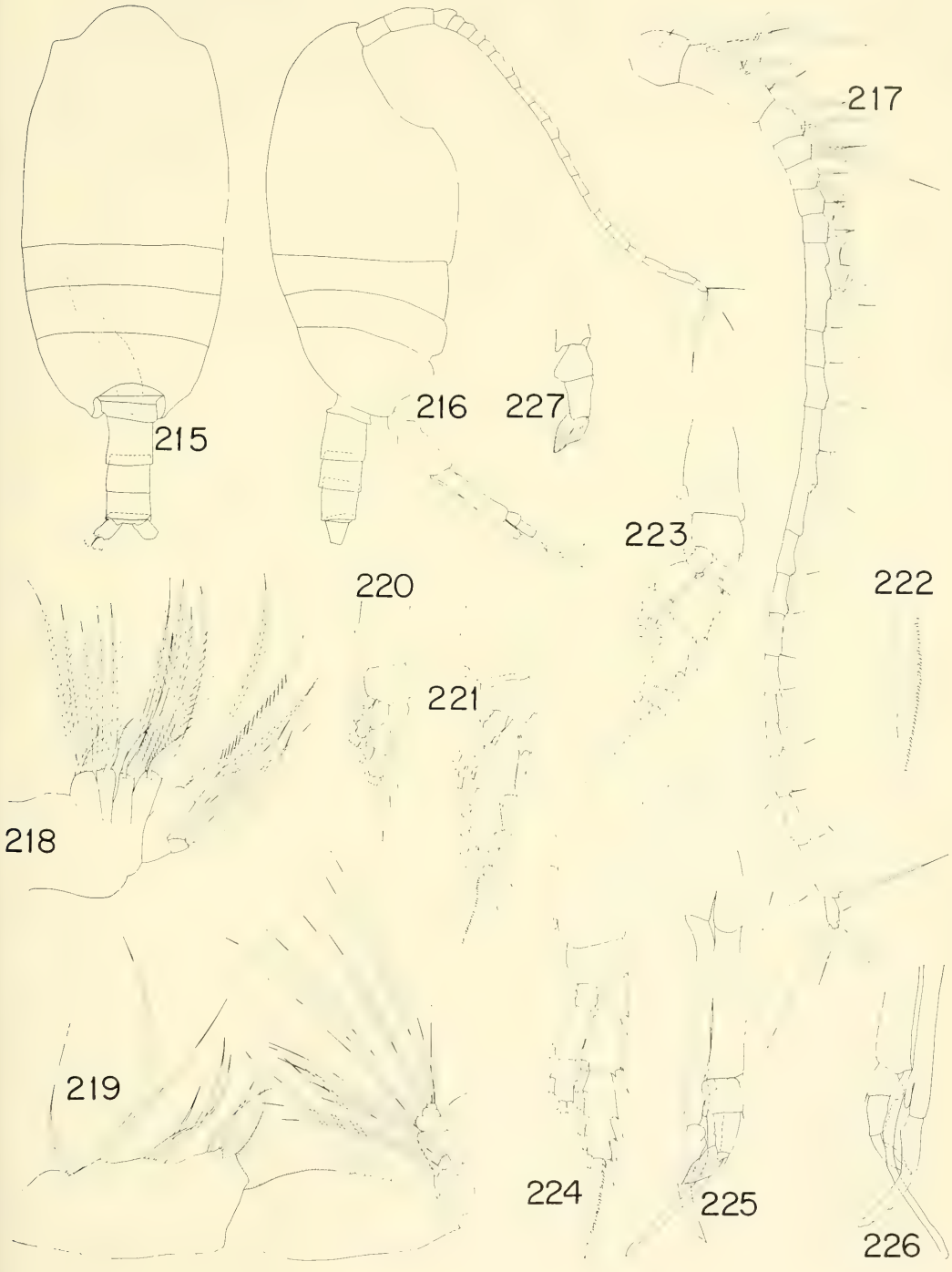
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Plate XII

Undinella compacta n. sp., female

Figure 228. Dorsal
Figure 229. Lateral
Figure 230. Right antennule
Figure 231. Antenna
Figure 232. Mandible palpus
Figure 233. Mandible blade
Figure 234. Maxillule
Figure 235. Maxilla
Figure 236. Maxilliped
Figure 237. First leg
Figure 238. Second leg
Figure 239. Third leg
Figure 240. Fourth leg
Figure 241. Fifth legs

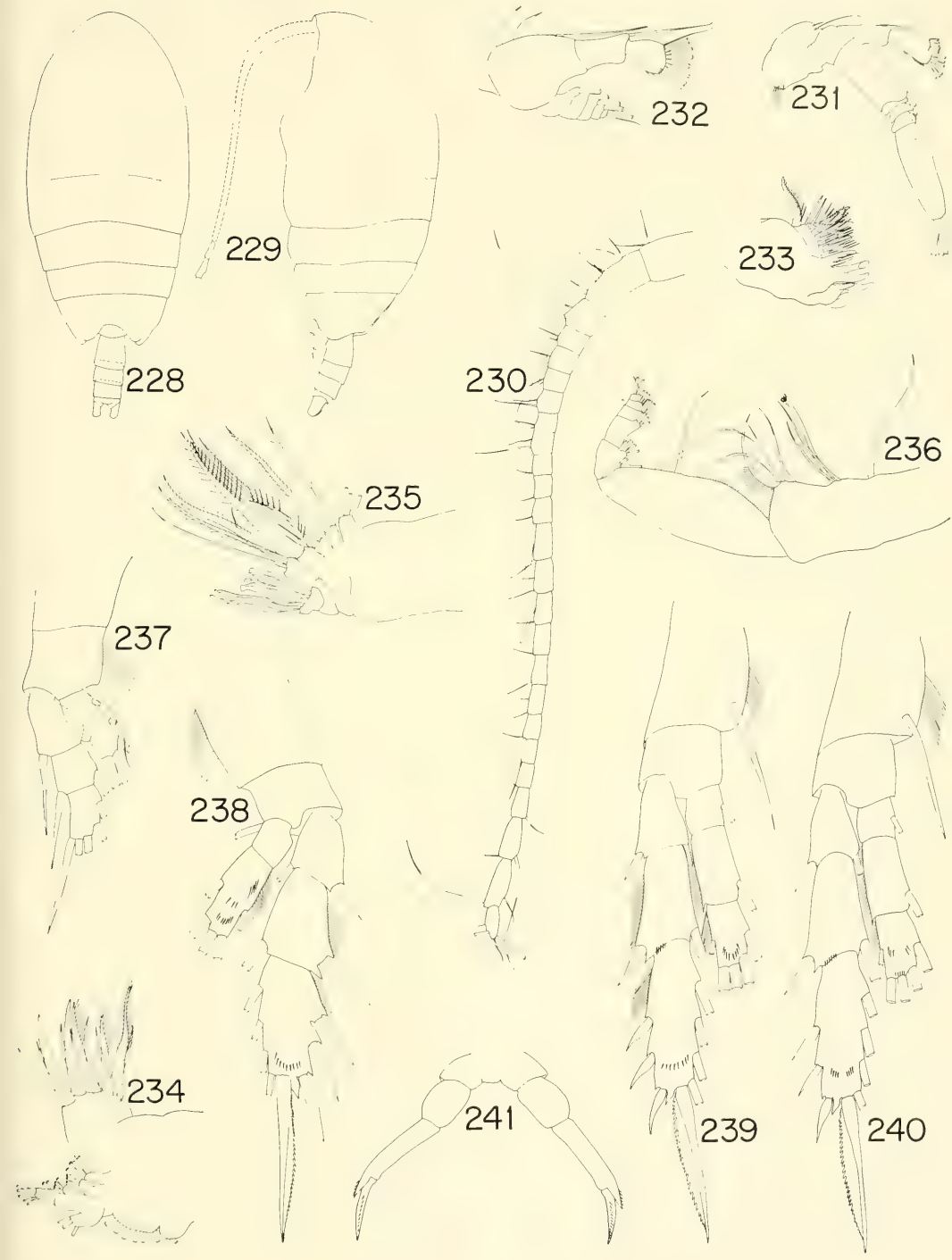
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Plate XIII

Undinella compacta n. sp., male

Figure 242. Dorsal
Figure 243. Lateral
Figure 244. Left antennule
Figure 245. Antenna
Figure 246. Mandible palpus
Figure 247. Mandible blade
Figure 248. Maxillule
Figure 249. Maxilla
Figure 250. Maxilliped
Figure 251. First leg.
Figure 252. Second leg
Figure 253. Third leg
Figure 254. Fourth leg
Figure 255. Fifth legs
Figure 256. Exopod of left fifth leg
Figure 257. Distal portion of right fifth leg

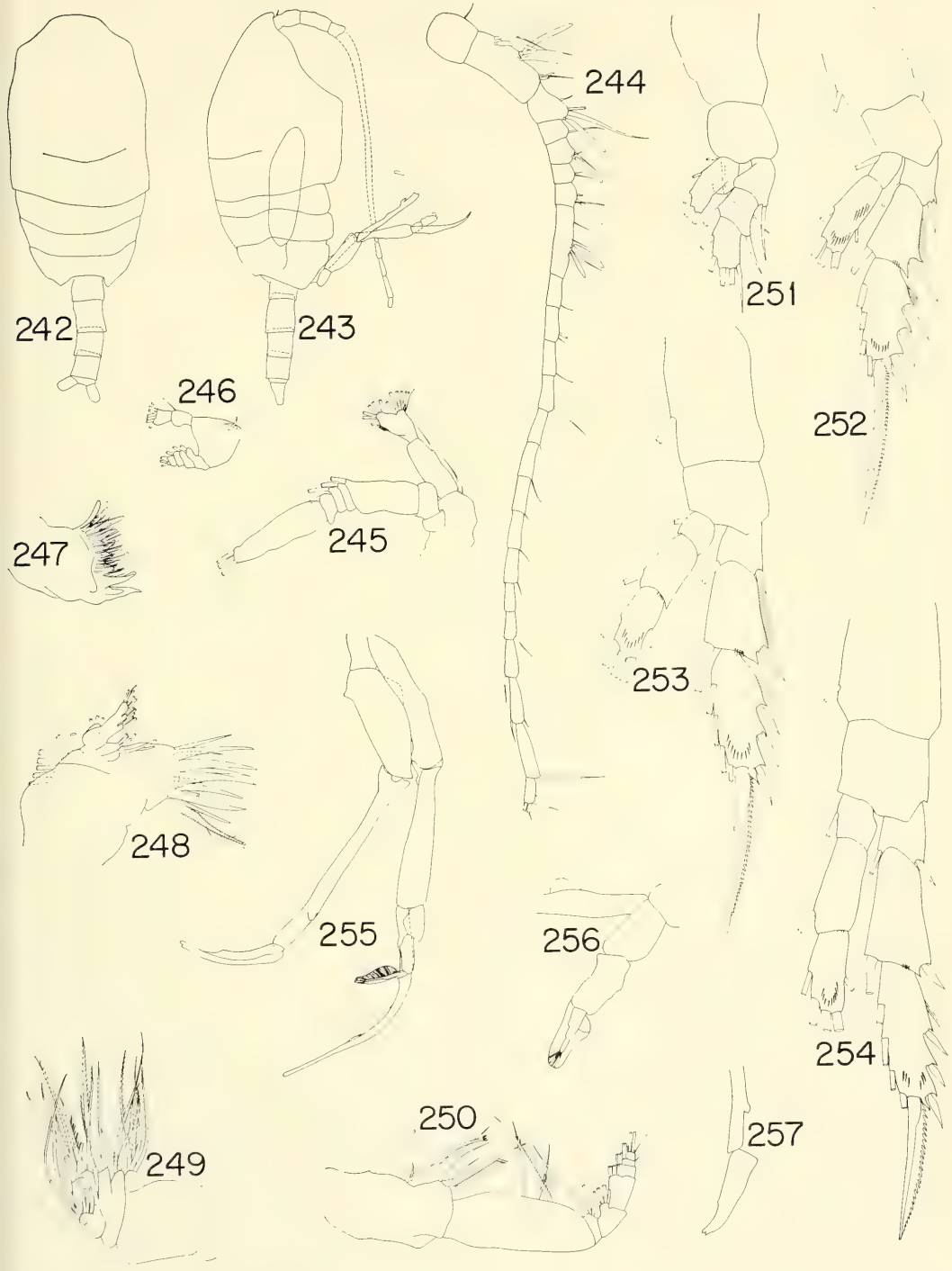
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Plate XIV

Undinelia hampsoni n. sp., female

Figure 258. Lateral
Figure 259. Second to fifth thoracic segments and abdomen, left side
Figure 260. Fifth thoracic segment and genital segment, ventral
Figure 261. Fourth and fifth thoracic segments and abdomen, right side
Figure 262. Fourth and fifth thoracic segments and abdomen dorsal
Figure 263. Anterior portion of head, lateral
Figure 264. Rostrum
Figure 265. Antennule
Figure 266. Antenna
Figure 267. Mandible palpus
Figure 268. Mandible blade
Figure 269. Maxillule
Figure 270. Maxillule, other side, spines on first inner lobe omitted
Figure 271. Maxilla
Figure 272. Fourth lobe of maxilla, other side

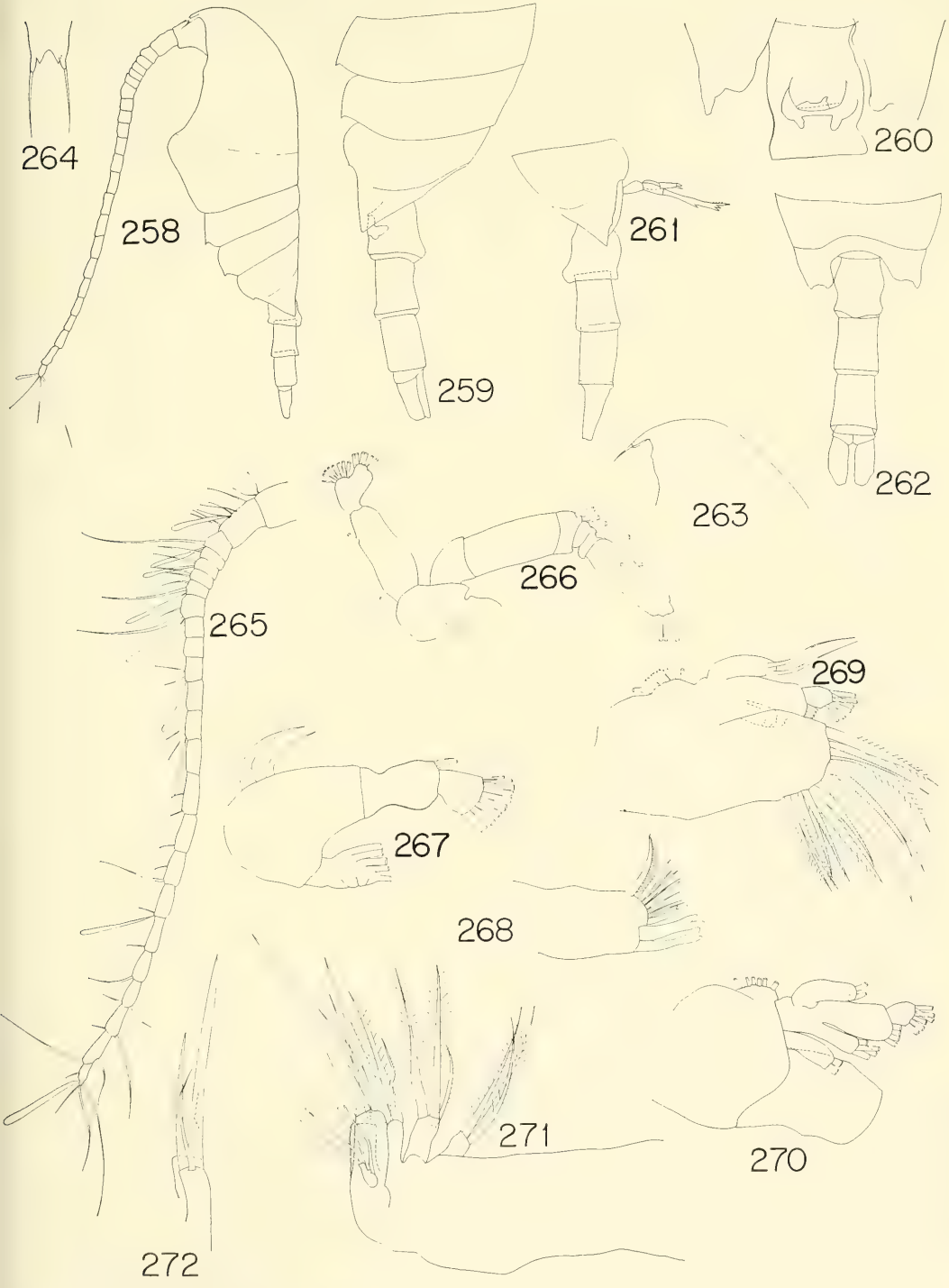
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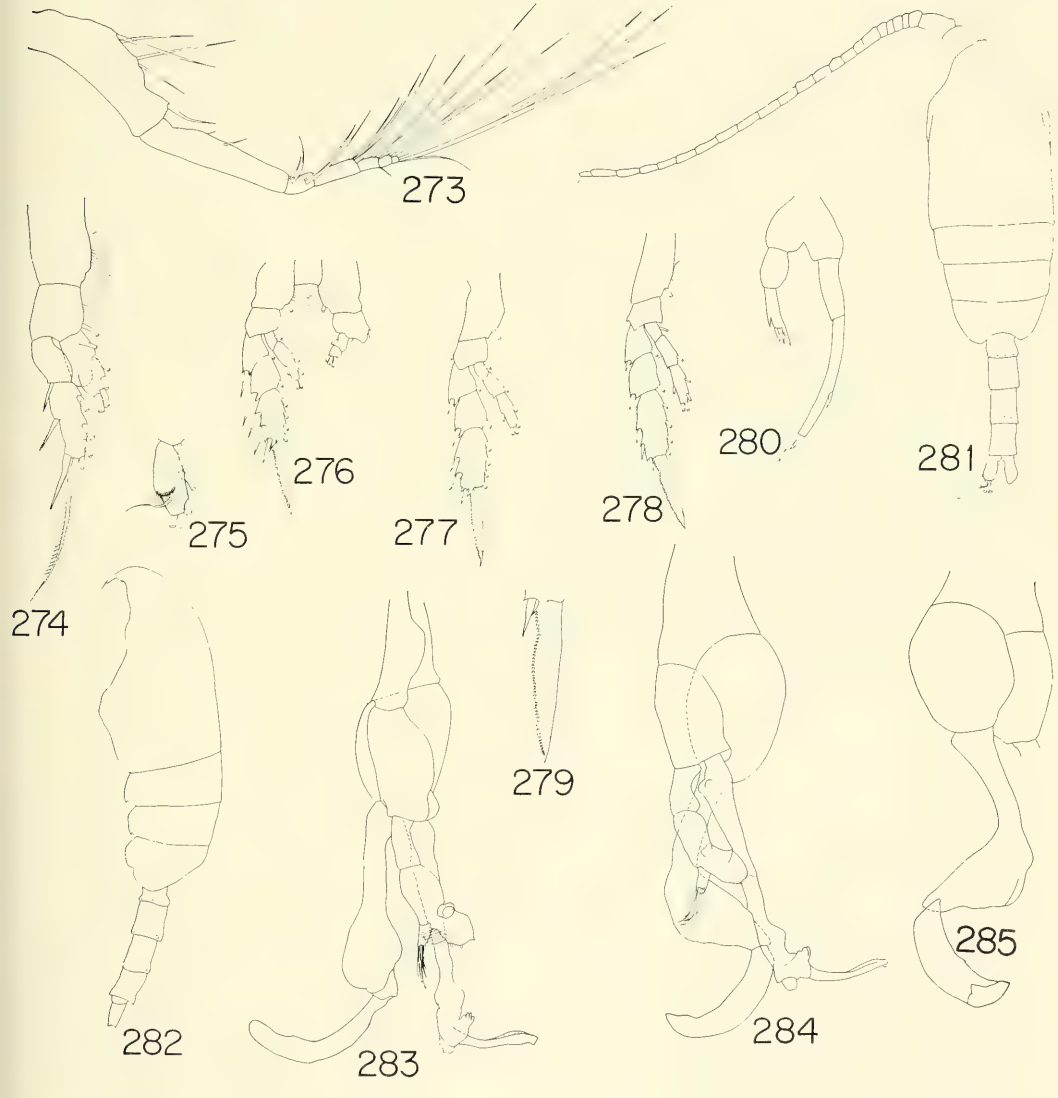
Plate XV

Undinella hampsoni n. sp., female (continued)

Figure 273. Maxilliped
Figure 274. First leg
Figure 275. Endopod of first leg, anterior
Figure 276. Second legs, anterior, exopod of left leg omitted, one endopod normal
Figure 277. Third leg
Figure 278. Fourth leg
Figure 279. Terminal spine of fourth leg
Figure 280. Fifth legs, posterior

Undinella hampsoni n. sp., male

Figure 281. Dorsal
Figure 282. Lateral
Figure 283. Fifth legs, from left
Figure 284. Fifth legs, another view
Figure 285. Right fifth leg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The Proterosuchia and the Early Evolution of the Archosaurs; an Essay About the Origin of a Major Taxon

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Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

Proceedings of the New England Zoological Club 1899–1948. (Complete sets only.)

Publications of the Boston Society of Natural History.

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THE PROTEROSUCHIA AND THE EARLY EVOLUTION OF THE ARCHOSAURS; AN ESSAY ABOUT THE ORIGIN OF A MAJOR TAXON

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ABSTRACT

After comments on several methodological and theoretical questions connected with the classification and the origin of major taxa, various hypotheses on archosaurian origins are discussed. A comparative survey of the characters of the early archosaurs, the proterosuchian thecodonts, shows that they are probably derived from the ophiacodont-varanopsid group of pelycosaurian synapsids. As the synapsids are known to have separated very early from the captorhinomorphs, and as the milleretids and younginids, which are captorhinomorph derivatives, are considered closely related to the origin of modern lepidosaurian orders, it is concluded that the two groups of diapsid reptiles, lepidosaurians and archosaurs, have quite different origins. A survey is also made of the present state of knowledge of the origin of the various archosaurian groups. The conclusion is that the final establishment of archosaurian orders as the dominant reptiles of the Jurassic and Cretaceous was the outcome of a gradual process, one which had an exploratory phase during the Middle and Upper Triassic. During this phase, various archosaurian lines of evolution developed, competing among themselves and with the therapsids in the exploitation of two basic food resources: green plants and animals. In the Upper Permian, the roles of plant-eaters and carnivores were mainly played by synapsids; from the uppermost Triassic to the end of the Cretaceous, they were mainly played by archosaurs. The origin

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of a major taxon is thus thought of as a long process involving several adaptive phases within the frame of the exploitation of food resources and of ecological competition. This process does not necessarily claim either the presence of special evolutionary processes or the acceleration of the rates of evolution in the transitional zone.

INTRODUCTION

The emergence and the rapid diversification of the archosaurian reptiles is one of the major events in the history of the vertebrates. During about 110 million years the terrestrial faunas of the world were dominated by the different dinosaur groups, which actually replaced, during Jurassic and Cretaceous times, most of the previously existing tetrapods in the exploitation of the varied terrestrial niches. During the same time another archosaurian group, the crocodiles, successfully occupied the freshwater, semi-aquatic, predaceous niche. Moreover, the Jurassic witnessed the first appearances of new major adaptive types among vertebrates: animals able to overcome the gravity barrier, the archosaurian order Pterosauria and the first birds, the latter being the most successful archosaurian derivatives surviving to the present time.

Disregarding the peculiar phenomenon of human evolution, we have to agree that the triumph of the dinosaurs and their relatives has been the major accomplishment in land vertebrate evolution, if we take as a criterion of evaluation the attainment of the greatest biomass by a single vertebrate group during the longest span of geological time. In this sense, the archosaurs have not been surpassed by any other vertebrate groups occupying the terrestrial environment. (The higher bony fishes in the seas have obviously surpassed the archosaurian achievement on land, but this does not matter in the present context.)

Many problems are posed by this empirical statement. The aim of science is to give causal explanations to observed phenomena, and we are far from being able to do this in the present case. However, we are at least able to draw the outlines of the framework within which such an explanation can eventually be attained. First of all, any metaphysical or pseudoscientific concept, such as "internal drive" or "phyletic senescence," must be excluded. Concepts of this kind are outside of scientific discourse, as they are untestable and do not sustain any kind of public demonstration of their existence. Instead, the phenomenon of archosaurian expansion and dominance may be thought of as part of a vaster and more complex phenomenon of life expansion within an entire ecosystem, since the rise of a land vertebrate biomass requires an even greater expansion of the biomass within the first trophic level, that of the green plants. However, one of the more important requirements for understanding such a phenomenon is a thorough and accurate knowledge, at the descriptive level, of the events leading to the dominance of archosaurs during the different phases of their evolution. In this sense, the first steps of archosaurian evolution and, indeed, the very emergence of the group are of paramount importance.

The first steps in archosaurian evolution took place during Triassic time, and the group attained dominance during the early Jurassic. The fossil record shows that the Triassic witnessed a major overturn in the distribution of roles in the food-web relationships: the roles of herbivores and carnivores during Permian and early Triassic times were mainly filled by synapsids, whereas during Jurassic and Cretaceous times, these roles were filled by archosaurs.

The Triassic, then, was the period during which the archosaurs became dominant. Once having achieved their dominance, they held it during two entire geological periods. However, the rise of the archosaurian orders was actually accomplished at the very end of the Triassic, and was a step-wise process, in which several lines

evolved and became extinct. The principal archosaurian roles were played during these first steps by taxa currently included in the order Thecodontia. One can say that the archosaurians had a first, exploratory radiation before their main one, a radiation that took place within this order of the thecodonts.

The very beginning of this exploratory radiation was developed during early Triassic times by a very primitive and atypical archosaur group, the Proterosuchia, usually grouped as a suborder of the Thecodontia. The proterosuchians are hence the stem archosaurs, the stock from which most of the later archosaur groups took their origin. An adequate understanding of them is thus essential for a good interpretation of all the further events of archosaurian evolution.

Knowledge of the Proterosuchia has been very unsatisfactory until recently. Fortunately, during the last ten years (and especially during the very last part of this period), descriptions of new materials and thought-provoking revisions have shed new light, thus helping us to reach a better understanding of the group. As usual in scientific progress, new knowledge leads to new problems, and our progress in the understanding of these primitive thecodonts poses several new questions. The general outlines of archosaurian evolution are now in need of a thorough revision, and the whole problem of the origin of this subclass must be approached in a new way because of the improvement of our knowledge of the Proterosuchia. Nevertheless, neither of these goals can be adequately achieved before a good assessment of the bearing of proterosuchian peculiarities on archosaurian evolution is available. The assessment of these peculiarities also poses a problem in classification. The aim of this paper is to stress the general evolutionary significance of the characters of this group of primitive thecodonts and to stress some methodological points that arise in our attempt to place them in an evolutionary classification.

As the stem group of a major taxon, the Proterosuchia set forth some interesting classification problems for the theory of evolutionary systematics, which will also be discussed in the following pages.

ACKNOWLEDGMENTS

The first draft of this paper was written in the Museum of Comparative Zoology of Harvard University during the autumn of 1966 as part of my work as a Guggenheim Fellow. I am much indebted to the John Simon Guggenheim Memorial Foundation for the opportunity of pursuing these studies, and to Dr. Ernest E. Williams, Dr. Alfred S. Romer, and Prof. Bryan Patterson for the facilities they afforded me during my stay in the Museum. Mrs. Ruth Romer and the late Dr. Tilly Edinger contributed in an invaluable way to make the time I spent in Cambridge pleasant and easy. As far as the content of this paper is concerned, I am indebted to illuminating discussions with Dr. Romer and to the critical comments on some of my views by Drs. Edwin E. Colbert, Alan Charig, Mario Bunge, George G. Simpson, Tilly Edinger, Ernst Mayr, Ernest E. Williams, Eviatar Nevo, William D. Sill, and José F. Bonaparte. In the revision of the manuscript, I received great help from Dr. Williams, Prof. Patterson, Dr. Richard Estes, and Dr. Robert L. Carroll, to all of whom I express sincere thanks.

FOUNDATIONS

Some theoretical points are worth stating before discussing our topic. Authors frequently disagree for the simple reason that the one is not aware of the underlying concepts of the other. This is especially true when the concepts are controversial in nature. As most of our argument deals with supraspecific taxa, it will be convenient to assess the sense we give to this concept.

A supraspecific taxon is not here thought

of as a mere artifact created to fulfill the aims of taxonomic practice. It is considered a natural group, a historico-spatial entity formed by various subordinate taxa connected among themselves by special evolutionary relationships: common origin, links of descent, and a common evolutionary role. The origin of a supraspecific taxon is not here assumed to be the outcome of special evolutionary processes. We take for granted that the known short-term processes of evolution at the species level are also the causal agents responsible for the establishment of major taxa over long-term evolutionary processes. But as the scale of the latter processes allows and requires more general descriptive concepts, we can also say that, in the emergence of supraspecific taxa, anagenesis, cladogenesis, and extinction are involved. The type of anagenesis here operating is the "open anagenesis" (Waddington, 1960) or arogenesis (Reig, 1963b). Arogenesis is associated with the acquisition of a new "basic general adaptive complex" (Simpson, 1959: 270). Other authors name these kinds of acquisitions "Erfindungen" (Rensch, 1947) or "key innovations" (Bock, 1965). It is commonly supposed that the emergence of these novelties is responsible for opening the possibility of exploiting new adaptive areas to the new taxon, thus promoting its splitting to fill up new ecological niches and situations (cladogenesis). We want to emphasize that the extinction of the groups previously exploiting the same ecological niches may be a triggering factor for the emergence of the new taxon. This extinction may also be thought of, however, as provoked by the rapidly evolving, and better adapted, emerging new taxon.

Another attribute of a supraspecific taxon is monophyly. As this concept is rather controversial, we will enunciate the two extreme possibilities for the fulfillment of this condition: a monophyletic group may be considered as either a group originating from a single ancestral species or, at the least, a group originating in a taxon of the same rank.

Supraspecific taxa originate by the differentiation from an original group of a new group showing new characteristics (Sharov, 1965). It has been generally assumed that in this process of the differentiation of a new group the shift of the evolving organisms into a new adaptive zone is a necessary condition. Such a shift would then involve a threshold effect, and the rate of evolution would be accelerated in the transitional area. Simpson (1953) named this supposed phenomenon "quantum evolution," pointing out that the period of rapid transition involved in such a process may serve to establish comparatively nonarbitrary divisions among major taxa (Simpson, 1961). Gisin (1966), in developing the same ideas, emphasizes that the "evolutionary quantum" affords the main criterion for the definition of taxonomic groups. As far as the theory of classification is concerned, he defines the concept of evolutionary quantum as follows: "Un quantum n'est pas la somme de toutes les différences, mais celle des caractères clefs développés lors de l'évolution quantique du groupe, autrement dit, les caractères sont pesés en fonction de leur signification évolutive" (Gisin, 1966: 4). Gisin refers to these ideas as a "quantum theory of taxonomy," a development of his former "synthetische Theorie der Systematik" (Gisin, 1964). It seems obvious to the present author that all these concepts are better considered as part of the approach already named "evolutionary taxonomy" (see Mayr, 1965).

We believe that these principles give a sound basis for the assumption that natural groups have (or had, in the case of extinct groups) a real existence in nature as objective, historico-spatial collective entities, their unitary character being given by evolutionary relationships linking their different subordinate constituents. Nevertheless, these natural groups (having existence in the ontic level; see Bunge, 1959) are not

to be confused with the taxon-concepts we construct about them (existing in the cognitive or conceptual level). Systematists hypothesize that a given set of species belongs to a supraspecific taxon, that a constructed taxon-concept matches a natural taxon. When we say that a given number of species of Lower Triassic thecodonts are to be placed together in the suborder Proterosuchia, we are dealing with a taxon-concept (the suborder Proterosuchia) that we construct for a taxon we believe to have existed in nature. In this sense, the construction of a taxon-concept is equivalent to the statement of a hypothesis (Reig, 1968).

It must be stressed that, as with any scientific hypothesis, these evolutionary-taxonomic hypotheses may never be claimed to have reached a status of certainty after having been "proved." These hypotheses may be stronger or weaker, more or less well founded, but they can never be transformed into a fully certain piece of knowledge, certainty not being at the core of the scientific way of thinking. Nevertheless, this assessment does not obviate the necessity of trying to make our hypotheses match as closely as possible the events for which they are erected. The likelihood that an hypothesis closely approximates natural events will be greater if it is able to support testing procedures, if it has a high explanatory value, and if its predictions are infalsifiable (see Popper, 1959; Wilson, 1965). If the hypothesis fails to fulfill these requirements, clearly it must be rejected as a tool for understanding natural events.

By the very nature of paleontological evidence and of taxonomic-phylogenetic inference, we must admit from the start that fully satisfactory testing procedures for this kind of hypothesis have not yet been developed (for an interesting and thought-provoking discussion of this topic see Goudge, 1961). In most cases, in order to accept it, we must take refuge in its heuristic value or in such attributes as its internal coherence or accordance with available scientific knowledge. This means that the foundations of our argument could be very weak if we are not careful to clarify our taxonomic concepts as far as the available evidence and theory permit.

As with any concept, the taxon-concepts have intension (connotation) and extension (denotation). The intension of a taxon-concept is the set of peculiarities that determine its own nature, that is, the set of characters that distinguishes it from others. Its extension is the set of subordinate taxa that belong to it.

The taxon-concepts are polythetic concepts, as defined by Beckner (1959; Beckner named these kinds of concepts "polytypic concepts," and the name "polythetic" was introduced later by Sneath, 1962). For a better understanding of the nature of polythetic concepts, see also Sokal and Sneath (1963). Membership in a polythetic group is not decided by the complete sharing of a set of sufficient and necessary features. Sufficient and necessary properties are useful for classifying static entities, but not evolving organisms. In other words, any taxon-concept, for the very reason that it is intended to approximate an evolving entity, must be defined by reference to a set of characters that are assumed to be evolving in the frame of the taxon itself. Thus no claim is to be made that any member of the taxon must present all the relevant characters in the defined state, nor that any form must necessarily belong to it because it possesses one or a few of the stated characters.

Acceptance of these points makes it possible to understand why the Proterosuchia are to be considered archosaurs in spite of the fact that they lack many of the relevant archosaurian peculiarities, such as the full development of an otic notch or the habitually upright stance, and why the euparkeriids need not necessarily be considered proterosuchians, although they share with them some primitive characters.

Yet a taxon-concept cannot be a full polythetic class in the sense of the third

condition pointed out by Beckner, a condition asserting that membership in a particular aggregate does not of necessity require the possession of a given character. Actually, the intension of a taxon-concept must include one character or a limited number of characters, the possession of which is necessary for membership in the said concept. Otherwise, our theoretical assumption that a taxon evolves through the acquisition of defined "key innovations" is not fulfilled.

These foundations may be considered the theoretical and formal tools for approaching our topic within the framework of evolutionary systematics. We think the approach of evolutionary systematics has greater depth, is far more explanatory in nature, and accords better with modern evolutionary thought than do others, such as the cladistic approach (e.g., Hennig's "phylogenetisches Systematik") or the neo-Adansonian phenetic one.

THE EXTENSION OF THE PROTEROSUCHIA-CONCEPT

The first point to make clear in our attempt to elucidate the taxon-concept involved in the name "Proterosuchia" is the assessment of its extension. Though some sort of circular reasoning is unavoidable, it seems evident that the inferential process that leads to the construction of a taxon-concept begins with the failure to assign certain taxa to existing taxa of higher rank, thus revealing the existence of a previously unknown taxon. The concept of this taxon is now constructed on the basis of a need for a group to contain certain definite subordinate constituents. Needless to say, it is the peculiarities of the subordinate members that fail to find a place in existing taxa that indicate that these members need to be referred to a new taxon. However the intension of the latter can only be fully assessed after it is clear which are its members.

Charig and Reig (in press) have made an extensive survey of the genera to be included within the Proterosuchia and have discussed Hughes's broad conception and interpretation of this taxon (1963). It is unnecessary to repeat here the arguments developed in that paper, but a summary of the conclusions and further discussion of some points are relevant to the present topic: that Proterosuchia include only, so far as is presently known, one Upper Permian and several Lower Triassic genera. Most Lower Triassic archosaurs are proterosuchians, the only exceptions being *Mesorhinosuchus*, *Euparkeria* (including *Browniella*), and the doubtful *Wangisuchus* and *Fenhosuchus*. Some Middle and Upper Triassic archosaurs occasionally referred to the Proterosuchia, such as *Rauisuchus*, *Dasygnathoides*, *Hoplitosuchus*, *Saurosuchus* and *Stagonosuchus*, are well enough known to be excluded from this group (Reig, 1961; Charig and Reig, in press).

All the known proterosuchian genera seem clearly to fall into two distinct subordinate taxa of family rank, for which it is advisable to use the names Proterosuchidae and Erythrosuchidae. The former is the older, more primitive, and more aquatic group. The latter family is almost surely derived from the proterosuchids, appears later in the fossil record, is more advanced, and seems to have been composed of largely terrestrial carnivores.

The Proterosuchidae include the following genera: *Archosaurus* (1 species, from the Upper Permian Russian Zone IV); *Chasmatosuchus* (2 or 3 species, from the Russian Zone V, lowermost Triassic); *Chasmatosaurus* (Figs. 1, 3, 5) (3 or 4 species: one in the *Lystrosaurus* Zone, lowermost Triassic, South Africa, another in beds of the same age in Sinkiang, China, another in the Chinese Ermaying Series, late early Triassic, and a probable fourth unnamed species in the Panchet Series of Bengal); *Proterosuchus* (1 species, probably from the *Procolophon* Zone, middle

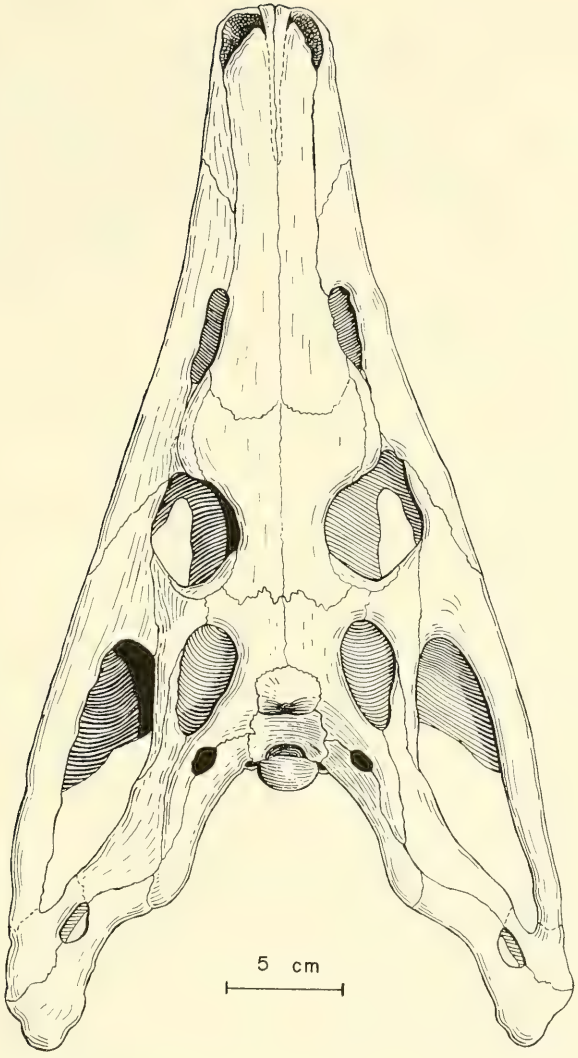

Figure 1. Dorsal view of the skull of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

Lower Triassic of South Africa); and *Elaphrosuchus* (1 species, from the *Lystrosaurus* Zone, South Africa).

The Erythrosuchidae includes the following genera: *Garjainia* (Fig. 2) (1 species, from the Russian Zone V, lowermost Triassic); *Erythrosuchus* (1 species, from the *Cynognathus* Zone, late early Triassic, South Africa); *Vjushkovia* (Fig. 4) (1 species, from the Russian Zone VI, late early Triassic); and *Shansisuchus* (1 or 2 species, from the Chinese Ermaying Series, late early Triassic).

Cuyosuchus (1 species, Cacheuta beds, Lower Triassic, Argentina) must be considered as Proterosuchia *incertae sedis*, as the material is not sufficient for family allocation. *Ankistrodon*, *Arizonasaurus*, *Dongusia*, *Seemania*, and *Ocoyuntaia* are generic names applied to material that may prove to be referable to the Proterosuchia, but which must be considered

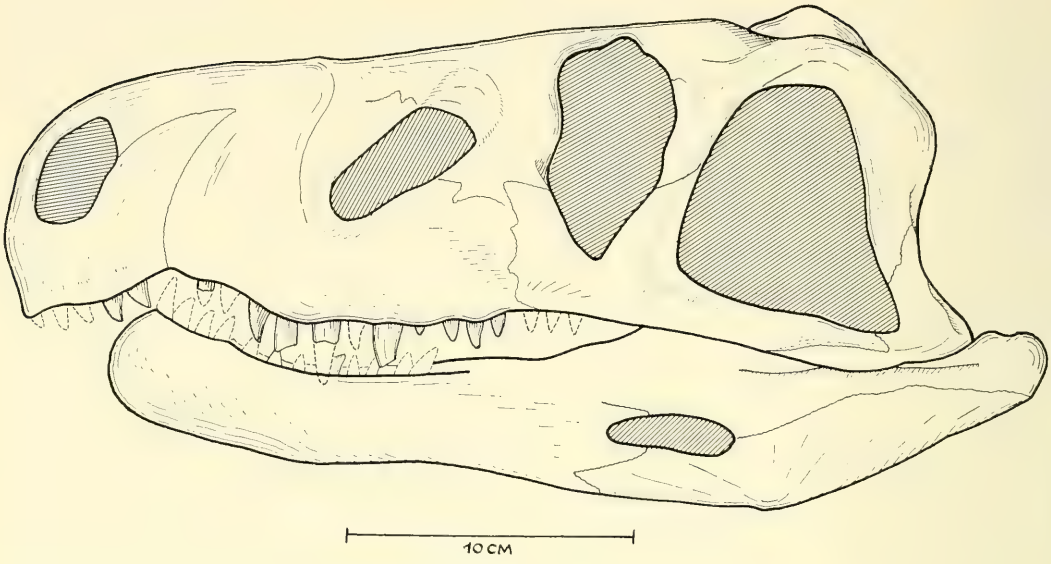

Figure 2. Lateral view of the skull of *Garjainia prima* Ochev. (From Ochev.)

nomina dubia for the present because the specimens are extremely fragmentary.

As these last remarks imply, not all the above-mentioned genera are really well known, and some are based on material too incomplete for adequate knowledge of all relevant characters. All evidence considered, however, we have a fairly good knowledge of at least the genera *Chasmatosaurus, Erythrosuchus, Vjushkovia, Shansisuchus,* and *Cuyosuchus,* from all of which a good part of the postcranial skeleton is known. The other genera that permit family allocation are known from less complete material. They are very useful, however, either to infer phylogenetic conclusions, as in the case of *Elaphrosuchus* and *Garjainia,* or to improve knowledge of the temporal and geographical distribution of the groups concerned.

Nevertheless, we must admit that we know only a very small part of the actual proterosuchian array, and this must be carefully kept in mind when discussing early archosaur evolution. It must be taken for granted that many proterosuchians existed that are at present unknown, and that among them might lie the direct ancestors of later archosaurs, which are not easily to be detected among the forms we know at present. This kind of assumption is the very basis of paleontological inference.

THE INTENSION OF THE PROTEROSUCHIA-CONCEPT

The Proterosuchia are such a puzzling group that von Huene was inclined, in one of his first works (1911), to place one of the included genera, *Erythrosuchus,* in an order of its own, sharing pseudosuchian and pelycosaurian features. As stressed by Hughes (1963), they combine some truly archosaurian peculiarities in the skull and other parts, with primitive, non-archosaurian characteristics in the limbs and girdles. As we shall see below, some non-archosaurian features are also present in the skull structures.

Hughes made a careful analysis of the peculiarities of the Proterosuchia, but he emphasized primarily postcranial morphology. Romer (1956, 1967), on the other hand, pointed out the significance of very

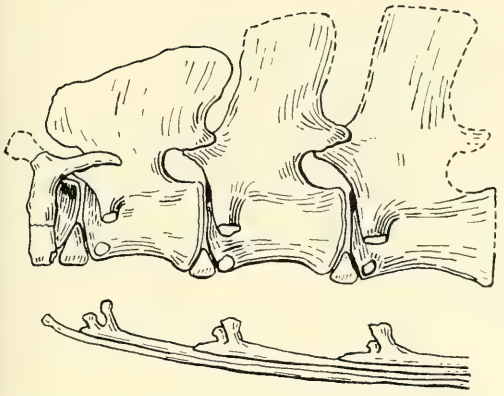

Figure 3. Cervical vertebrae and ribs of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

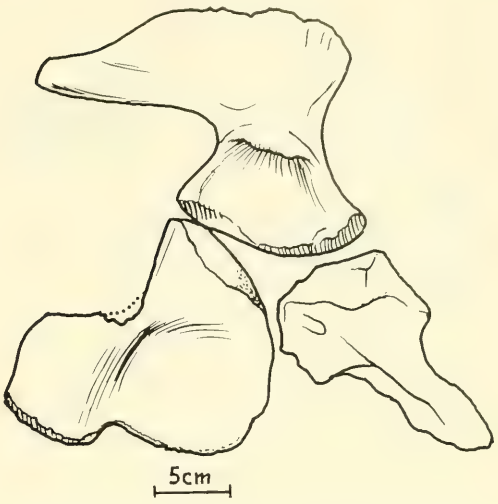

Figure 4. Lateral view of the pelvis of *Vjushkovia triplicostata* von Huene. (From von Huene.)

peculiar proterosuchian skull characters, neglected by Hughes and other authors. Charig and Reig (in press) list the state of many characters in this taxon, but they do not discuss thoroughly their evolutionary significance. A further analysis, therefore, seems necessary.

Statement and analysis of the proterosuchian character-states

Following Sokal and Sneath (1963), we shall use the character-state terminology in our present analysis. For these authors, a character is a variable that can occur in different states from one kind of organism to another. These character-states are the relevant features that taxonomists deal with in comparing different taxa. For instance, "dermal ossifications" is a character, and "dermal ossifications absent" is a character-state.

Since they belong to a taxon of higher rank, the subclass Archosauria, the Proterosuchia have a set of character-states shared by all archosaurs. We shall refer to this set of character-states as the "All-Archosaurian set of character-states" (*AA*). This *AA* set represents the intension of the taxon-concept Archosauria, and should not afford a relevant basis for elucidating the concept of Proterosuchia, though its assessment is very important to support the inclusion of the Proterosuchia in the Archosauria and for an enquiry regarding the origin of the whole subclass. The following list includes the character-states that we consider as belonging to this set:

i) Two-arched skull (diapsid condition)
ii) Antorbital fenestra present
iii) Mandibular fenestra present
iv) Laterosphenoid ossified
v) Skull metakinetic
vi) Quadrate-squamosal articulation moveable
vii) Supratemporal and tabular bones absent
viii) Posttemporal fenestrae small
ix) Vertebrae not notochordal
x) Ribs with capitulum and tuberculum
xi) Rib facets of dorsal vertebrae on transverse processes, becoming closer to a complete fusion posterad
xii) Capitular facets for cervical ribs situated well anteriorly and ventrally on the centrum; tubercular facets for the same ribs at the tip of transverse process
xiii) Posterior limbs longer than anterior (limb disparity)

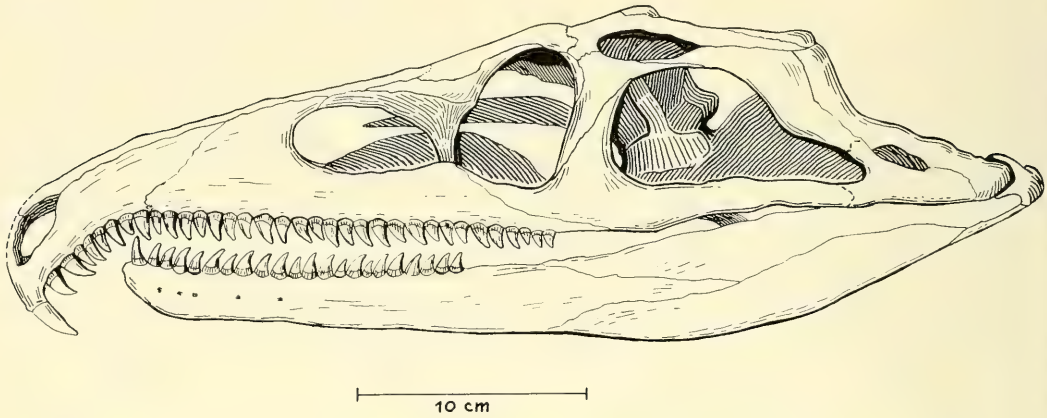

Figure 5. Lateral view of the skull of *Chasmatosaurus vanhoepeni* Haughton. (From Broili and Schröder.)

Some allegedly characteristic archosaurian character-states, such as upright stance and bipedalism, are not included in this list. As has been suggested by Charig (1965), they are neither characteristic nor widespread archosaurian features.

The core of our discussion should be connected with those character-states that would help to define the Proterosuchia as distinct from other taxa included in the Archosauria. These character-states may be grouped in four different classes: (a) the All-proterosuchian-No-other-archosaurian set of character states (*AN*), which includes peculiarities shared only by the proterosuchians, absent in any other archosaurian taxon; (b) the Some-proterosuchian-No-other-archosaurian set (*SN*), comprising characters that are present in the described state only in some of the proterosuchians, while present in a different state in other proterosuchians and in all the other archosaurs; (c) the All-proterosuchian-and-Some-other-archosaurian set (*AS*), including character-states shared by all the members of the extension of the Proterosuchia, but also present in some other non-proterosuchian archosaurs; (d) the Some-proterosuchian-and-Some-other-archosaurian set (*SS*), referring to those character-states shared by some, but not all the members of the Proterosuchia, and also by some, but not all, archosaurian groups not belonging to the Proterosuchia.

The following list attempts to synthesize the relevant character-states of the Proterosuchia. The letters preceding each statement refer to the above-defined sets.

1. (*AS*) A single median postparietal bone present
2. (*AS*) Small postfrontal bones present
3. (*SN*) A small pineal foramen present
4. (*AN*) A typical otic notch not present
5. (*AN*) The posterior border of the infratemporal fenestra nearly straight (without the V-shaped contour characteristic of most archosaurs)
6. (*AS*) The jaw articulation well behind the level of the occiput
7. (*AS*) Antorbital fenestra of moderate size, not opening as a part of a more extended, basin-like depression
8. (*AS*) Nares of moderate size, subterminal, fairly well separated from the antorbital fenestra
9. (*AS*) Pterygoids not meeting in the midline, bordering a long and narrow interpterygoid vacuity extending forward between the vomers

10. (*SS*) Palate with teeth in the pterygoid flanges
11. (*AN*) Occipital plane rather concave, slanting forward towards the skull table
12. (*AS*) Prefrontal bones large, projecting laterally to form a ridge that makes an abrupt limit between the roof of the skull and the lateral antorbital region
13. (*AN*) Marginal teeth isodont and acrodont or subthecodont in implantation
14. (*SS*) Intercentra usually present behind the axis, more commonly between the cervical vertebrae
15. (*AS*) Gait quadrupedal
16. (*AN*) Propodials horizontal in position (sprawled stance)
17. (*AN*) Posterior limbs moderately longer than the front ones (primitive limb disparity)
18. (*AN*) Femur bearing a large internal trochanter
19. (*AN*) Intertrochanteric fossa of the femur present
20. (*SS*) Humerus with wide and twisted ends
21. (*AN*) Pes with mesotarsal ankle joint (proximal tarsals without specializations)
22. (*AS*) Iliac blade with anterior spine absent or only moderately developed
23. (*AS*) Posterior expansion of the iliac blade narrow and long
24. (*AS*) Acetabula completely closed, only moderately excavated, and relatively far apart one from the other
25. (*AS*) Pubis and ischium comparatively short
26. (*AS*) Coracoids large
27. (*SN*) Scapulae broad and short
28. (*AS*) Dermal elements of the pectoral girdle well developed
29. (*AS*) Dermal armor of any sort absent

From the above list of character-states, interesting conclusions can be drawn, but it is first necessary to make a brief analysis of them.

(1) The possession of postparietal bones (Fig. 1) (interparietal, dermosupraoccipital) is a primitive condition for reptiles, and is widespread in such primitive groups as the cotylosaurs, the pelycosaurs, the eosuchians, and the millerettids. This character-state is shared by all the genera assigned to the proterosuchia, in the form of an unpaired postparietal. However, this is not an exclusive proterosuchian condition among the archosaurs, as a postparietal is also present in the pseudosuchian thecodont *Euparkeria*.

(2) Postfrontal bones (Fig. 1) are also present in most primitive reptile groups and in all the proterosuchians so far known. As in the former case, other non-proterosuchian archosaurs retain this primitive state, as postfrontals are present not only in *Euparkeria* but also in the phytosaurs, the stagonolepidid pseudosuchians, and the rhamphorhynchoid pterosaurs.

(3) A pineal foramen is, as far as is known, present only in all the known specimens of the erythrosuchid genus *Erythrosuchus*, in the primitive erythrosuchid *Garjainia* (see Tatarinov, 1961: 121), and in one of three known skulls of *Chasmatosaurus*. Other proterosuchian genera either have been reported as not possessing this character, or cannot be checked due to the nature of the material. Among other non-proterosuchian archosaurs, this character is absent, save in one doubtful genus, *Mesorhinosuchus* (=*Mesorhinus auct.*), currently considered the only Lower Triassic phytosaur. We are also dealing here with a very primitive state of a character, present as such in the earliest reptilian groups.

(4) Romer pointed out (1956, 1967) the absence of a typical otic notch in the Proterosuchia. He based his statement on the genera *Chasmatosaurus* (Fig. 5) and *Erythrosuchus. Garjainia* (Fig. 2), *Shansisuchus,* and *Vjushkovia* give support to the same view. The latter genus has indeed been reconstructed by von Huene (1960) as having a well-developed otic notch, but this reconstruction is purely hypothetical and is not supported by the morphology of the surrounding parts. Tatarinov (1961) has indicated that the posterior border of the infratemporal opening was straight in *Vjushkovia,* as in *Erythrosuchus,* a feature correlated, in other proterosuchian genera, with the absence of a defined otic notch. In all proterosuchian skulls, therefore, the construction of the otic region is very primitive. This recalls the pelycosaurian and captorhinomorph condition and differs from all remaining archosaurs and from lepidosaurs (including millerettids and eosuchians, in which a distinct lepidosaurian otic notch is clearly present). In all non-proterosuchian archosaurs the otic notch is clearly defined by a curved posterior border of the quadrate and by a projection of the squamosal, which extends posteriorly above the head of the quadrate to form the dorsum of the notch. The character-state "absence of the otic notch" hence belongs obviously to the *AN* set.

(5) Linked with the otic notch is the shape of the posterior border of the infratemporal fenestra. The V-shaped contour of this border, with the apex of the V facing forward, is common to all the non-proterosuchian archosaurian genera (save those with secondary modifications from a primitive V-shaped condition). In connection with the posterior position of the mandibular articulation, the quadrate of the proterosuchians slants sharply backwards. The ascending ramus of the quadratojugal and the descending ramus of the squamosal follow the quadrate in this position. In more advanced archosaurs, the jaw articulation moved forward, apparently in connection with the development of a more efficient biting mechanism (Ewer, 1965), and the quadrate acquired a more vertical position. In this position of the quadrate, the V-shape of the quadratojugal and squamosal arms is obligatory, and, consequently, room is developed for an otic notch, further enlarged by the backward projection of the squamosal. The proterosuchian condition of this character is again a primitive one, as this is the state shown by the pelycosaurs, especially by the varanopsid pelycosaurs. The assumption that this condition is shared by all the proterosuchians is safe, and the same is valid for character-state 4, as it is present both in primitive (*Chasmatosaurus*) and advanced genera in which the skull is known (*Erythrosuchus, Shansisuchus*). Therefore, this is to be considered an *AN* character-state.

(6) As far as the position of the jaw articulation is concerned, this character obviously belongs to the same cluster as the two previously described. All the proterosuchian skulls so far known show a backward position of the suspensorium (Figs. 1, 2, 5), the articular condyles for the mandible lying in a line well posterior to the line of the occipital condyle. This condition is distinctly different in the non-proterosuchian archosaurs, save the primitive crocodile *Proterochampsa* and, in a lesser degree, some phytosaurs. Character-state 6 belongs therefore to the *AS* class. Romer (1967) pointed out that this long-jawed condition is characteristic of very primitive reptiles and is reminiscent of the captorhinomorph skull architecture. In primitive pelycosaurs of the ophiacodont-varanopsid group this character-state is even more pronounced, but both the millerettids and the eosuchians are more progressive in this respect.

(7) The presence of an antorbital fenestra is a characteristic archosaur character-state. It is safe to consider the

condition of the character in the proterosuchians as primitive, as in them the fenestra does not reach a large size and, especially, as it does not lie in a depression with sharp borders, as is the case in most other thecodonts and other archosaurs. Though the function of this fenestra is not completely clear (Ewer, 1965; Walker, 1961), it is obvious that whatever its function may have been, its increase in size, and the development of a basin-like structure to contain it are to be considered as an intensification of the function; the structure was not fully developed in the proterosuchian level of archosaurian evolution. The described proterosuchian state of this character seems to be shared by all the known skulls (Figs. 2, 5) referred to this taxon, with *Shansisuchus* as an atypical example, since this genus has the peculiarity (also present in some saurischian dinosaurs) of having an additional opening, though not a basin-like depression. *Vjushkovia* has been restored by von Huene with a great antorbital opening, but again this seems clearly to be a quite tentative reconstruction, as most of the borders of the fenestra are not preserved in the known specimens. The fact is that other, non-proterosuchian, archosaurs share this state of the character, as is shown in the primitive crocodile *Proterochampsa*, in the peculiar pseudosuchian *Rhadinosuchus* (=*Cerritosaurus*), in *Clarenceia*, and in the phytosaurs. This character-state is therefore to be considered as belonging to the *AS* class. It is indeed very suggestive that an antorbital fenestra, elsewhere only an archosaurian character-state, is present in the varanopsid pelycosaurs (Olson, 1965, and see also below).

(8) The described state of the external nares is shared by all the proterosuchian genera (Figs. 1, 2, 5). More advanced thecodonts usually have the external nares larger and nearer to the antorbital vacuity, or else posterior in position (phytosaurs). Subterminal, small nares well separated from the antorbital opening are also present in *Rhadinosuchus* and *Clarenceia*, and the situation in *Euparkeria* is best considered reminiscent of the proterosuchian state. This character-state must therefore be grouped in the *AS* category.

(9) This character-state is inferred from the condition in *Chasmatosaurus*, the only proterosuchian in which the palate is well known. Inasmuch as the same condition is shared in such a probable erythrosuchid-derivative as *Euparkeria*, it is safe to conclude that this state was widespread among the proterosuchians. Among other archosaurs, it is shared not only by *Euparkeria*, but also by *Proterochampsa*, so that the character-state must tentatively be considered as belonging to the *AS* class.

(10) The presence of palatal teeth in the pterygoid flanges has been verified in *Chasmatosaurus* and *Proterosuchus* among the proterosuchids, but no erythrosuchid has given any evidence of them. Palatal teeth are known among archosaurs, other than proterosuchians only in *Euparkeria* and in *Proterochampsa* (Sill, 1967). This state of the character is obviously a primitive one, as palatal teeth are present in millerettids, younginids, procolophonids, pelycosaurs, and captorhinomorphs among the primitive groups. It must hence be placed, so far as present knowledge allows, in the *SS* class.

(11) This is a peculiar, primitive, and pelycosaur-like state of the occipital region. All the proterosuchian genera in which the character can be checked show this state clearly; it is especially evident in *Chasmatosaurus*. No other archosaur shows a similar condition, so that this feature is to be allocated to the *AN* class.

(12) This state of the prefrontal is not a proterosuchian peculiarity, as it is also characteristic of many thecodonts that are not proterosuchians and of some saurischians. The condition is also shared by some non-archosaurian reptiles, such as the

ophiacodont and varanopsid pelycosaurs. This fact suggests that we are confronting a primitive character-state that evolved slowly within the archosaurs. As it is shared by all the proterosuchians so far known, it must be placed in the *AS* class.

(13) In all proterosuchians so far known, the marginal teeth are isodont and either acrodont (proterosuchids) or subthecodont (erythrosuchids); true heterodonty and thecodonty are not clearly developed in either group. All non-proterosuchian archosaurs are definitely thecodont in tooth implantation, and their teeth are primitively heterodont or subheterodont. The proterosuchian condition is also a primitive one, widespread among the earliest reptiles and their first derivatives. This character-state must hence be placed in the *AN* class.

(14) Another primitive condition reminiscent of the seymouriamorph, captorhinomorph, pelycosaurian, and early lepidosaurian condition, is the presence of intercentra. This has been clearly demonstrated in the neck vertebrae of *Chasmatosaurus vanhoepi* (Fig. 3), and Young (1963) has described the same situation in the trunk vertebrae of *Chasmatosaurus yuani*. Neck intercentra have been reported in *Erythrosuchus*, but seem not to be present in *Shansisuchus*, *Garjainia*, *Vjushkovia*, and *Cuyosuchus*. In later archosaurs, intercentra have not been reported in any genus save *Euparkeria*, where they seem to be present all along the presacral region of the column. Another (abnormal) exception is the rauisuchid *Ticinosuchus*, which is alleged to have had an intercentrum associated with one of the caudal vertebrae (Krebs, 1965). We are dealing therefore with a feature of the *SS* class.

(15) The quadrupedal gait is, of course, a character-state shared by all the known proterosuchians, but obviously common, too, in many non-proterosuchian archosaurs, such as the euparkeriids, the rauisuchids and the stagonolepidids among the thecodonts, the crocodiles and phytosaurs, and many groups of saurischians and ornithischians. This is obviously a primitive reptilian feature, and must hence be placed in the *AS* class.

(16) The position of the propodials has been inferred by Hughes (1963) to be horizontal in the known proterosuchians. Nevertheless, Young's (1964) reconstruction of the skeleton of *Shansisuchus* shows the propodials in a vertical position, which is probably also reasonable. Completely sprawled legs would not have allowed large terrestrial animals such as the erythrosuchids to be successful predators, and the evidence seems to indicate that they had a time of success during the Lower Triassic. It is probable that all the proterosuchians had a sprawled stance most of the time, as indicated by the anatomical data, but that at least the advanced erythrosuchids could proceed in a largely upright stance for short distances. In any case, it is obvious that the proterosuchians sprawled more than any later archosaur, and that this state was shared by all the genera that afford relevant evidence in the girdle and limb skeletons. As stated by Ewer (1965), *Euparkeria* also seems to have had a sprawled stance, but this genus seems to have been far more advanced than the proterosuchians as far as locomotion is concerned. This feature can therefore safely be considered to be in the class of the *AN* character-state.

(17) This character-state is a typical archosaur one, though it has been exaggeratedly associated with bipedalism, which is not only not a widespread condition in archosaurs, but is not even a primitive archosaurian characteristic (Charig, 1965). Charig has named this condition limb-disparity, and though characteristically archosaurian, it must be noticed that this is also present in the ophiacodontid and varanopsid pelycosaurs. Limb disparity may be considered a preadaptation for

bipedalism, but is less marked in the Proterosuchia than in more advanced archosaurs. In the known cases, for instance, the humerus/femur ratio is never lower than 77.7 in the proterosuchians, and is always lower than 67 in the non-proterosuchian thecodonts. This might be therefore considered an *AN* character-state.

(18), (19) The possession of an internal trochanter and of an intertrochanteric fossa is alleged by Hughes (1963) to be a full indication of the sprawled position of the legs. As far as is known, all proterosuchian femora share in the possession of these characters. The pelycosaurs and captorhinomorphs share the same character-state, but none of the known non-proterosuchian archosaurs have either an internal trochanter or an intertrochanteric fossa. Hughes assumed that the Argentinian rauisuchid *Saurosuchus* shared the proterosuchian state of these characters, but this is a misinterpretation of the illustrations given by Reig (1961), as Charig and Reig (in press) have already made clear. These character-states hence belong to the *AN* class.

(20) The structure of the humerus is well known in *Chasmatosaurus* (Young, 1963), *Erythrosuchus*, *Shansisuchus*, *Vjushkovia*, and *Cuyosuchus* (Rusconi, 1961, wrongly described this bone in *Cuyosuchus* as the femur of the labyrinthodont *Chigutisaurus*). In all these genera the ends are twisted, but in the last they are not typically wide, as is the case in the other four genera. Humeri with wide and twisted ends are also present in the rauisuchid *Stagonosuchus* (von Huene, 1938; Boonstra, 1953) and in the problematic Argentinian Middle Triassic genus *Argentinosuchus* (Casamiquela, 1961). This may be considered a primitive character-state, as it is also present in the pelycosaurs and captorhinomorphs. In any case, the exception of *Cuyosuchus* and the presence of the same state in other non-proterosuchian thecodonts, indicate that it is convenient to place this feature in the *SS* class.

(21) The structure of the feet in the proterosuchians has been elucidated by Hughes (1963) with the help of new material. Work by Ewer (1965) and Krebs (1963, 1965) on *Euparkeria* and *Ticinosuchus* respectively, offers additional support to Hughes's conclusions. In the proterosuchians the foot anatomy is only known to an appropriate degree in *Chasmatosaurus* and *Erythrosuchus*, but it seems safe to infer that the condition in these genera was widespread among all the proterosuchians. The state is that of a tarsus without "crocodiloid" or "dinosaurian" specializations in the proximal tarsals (astragalus and calcaneum), and with a primitive, mesotarsal ankle joint. All other archosaurs show some type of tarsal modifications from this primitive condition, which is, by the way, like that in primitive lepidosaurians, such as *Youngina*, and in captorhinomorphs and pelycosaurs. All evidence indicates the convenience of placing this character-state in the *AN* class.

(22) The shape of the anterior spine of the iliac blade (Fig. 4) varies among the different proterosuchian genera from almost obsolete in *Chasmatosaurus* to moderately developed in genera like *Cuyosuchus*, but it is never highly developed, as it is in some pseudosuchians and "dinosaurs." The proterosuchian type of anterior spine of the ilium is very similar to that of the varanopsid pelycosaurs. At the same time, this same feature is also present in some non-proterosuchians, as is the case in *Euparkeria* and the rauisuchids, and for this reason it must be considered an *AS* character-state.

(23) The posterior spine of the iliac blade is long and narrow in all the known proterosuchian genera that afford evidence in this regard. Among the non-proterosuchian thecodonts, *Euparkeria* and the rauisuchids share the same condition, so

that this is also a character-state of the *AS* class.

(24) The fully closed condition of the acetabula is a proterosuchian character, associated with the amount of space between them; both conditions are related to the generally sprawled position of the posterior propodials. All the thecodonts show a closed acetabulum, and in most of them these are relatively far apart. Open and more closely approximated acetabula were developed in the saurischian and ornithischian dinosaurs in connection with the advanced bipedal stance. This is also an *AS* character-state.

(25) The relative length of the ventral pelvic bones varies within narrow limits in the proterosuchians, never reaching the development shown in more advanced archosaurs with triradiate pelves (Fig. 4). In the primitive forms the triradiate trend is only incipient, although it is more obvious in terminal forms like *Erythrosuchus*. In forms like *Chasmatosaurus* and *Cuyosuchus*, features of the very primitive puboischiadic plate can also be observed. *Euparkeria* shows in this respect a condition more proterosuchian than typically pseudosuchian, and *Ticinosuchus* seems to be transitional in this regard. This character-state must thus be considered to be in the *AS* class.

(26) Coracoids are known in *Chasmatosaurus, Cuyosuchus, Erythrosuchus, Shansisuchus* and *Vjushkovia*. In the first two they are obviously larger and more primitive than in the latter, but in any case, the proterosuchian coracoids are to be considered as large in comparison with those of most later archosaurs. Among the Pseudosuchia, large coracoids are present in *Euparkeria*, the rauisuchids *Ticinosuchus* and *Proterosuchus*, and the stagonolepidids. We must hence place this character-state in the *AS* class.

(27) The scapular blade is short and broad, and primitive in general shape, in both *Chasmatosaurus* and *Cuyosuchus* (Fig. 1). In the genera *Erythrosuchus, Shansisuchus*, and *Vjushkovia* it is higher and narrower, with both ends more expanded than the median "shaft." Short and broad scapulae are to be considered as primitive, and the shape of this bone in the erythrosuchids is obviously an improvement, which becomes more fully developed in pseudosuchians and later archosaurs. This character-state is to be placed in the *SN* set.

(28) The presence of dermal elements of the pectoral girdle is now known in *Chasmatosaurus, Shansisuchus, Erythrosuchus, Vjushkovia*, and *Cuyosuchus*. The first had been assumed to have a clavicle and interclavicle because of the presence of these bones in more advanced thecodonts (Hughes, 1963), but Young (1963) actually found a clavicle associated with other bones of *Chasmatosaurus yuani*. It is safe to conclude that dermal bones of the shoulder girdle were present in all the members of the Proterosuchia. At the same time, this primitive feature is also shared by many pseudosuchians, such as the rauisuchids, the stagonolepidids, *Euparkeria*, and even *Ornithosuchus* (see Walker, 1964: 110). We are dealing therefore, with a character-state of the *AS* class.

(29) As far as dermal armor is concerned, the Proterosuchia, in lacking any indication of it, are clearly different from all other thecodonts (Charig and Reig, in press). The only doubtful case in this respect is *Cuyosuchus*, as among the original material some atypical scutes were found. Since these could belong to the labyrinthodont found associated with the Argentinian proterosuchian, it is better not to consider this case as an actual exception. Crocodiles, phytosaurs, and ornithischians have osteoderms, but they are missing in saurischian dinosaurs (see below) and pterosaurs, so that the present condition must also be considered as an *AS* character-state.

Evolutionary and taxonomic significance of the proterosuchian character-states

The foregoing analysis indicates that the Proterosuchia-concept is not a fully polythetic one, as only five among twenty-nine peculiarities are not shared by all the members of its extension. But, by the same token, it is not a monothetic concept. More significant is the fact that eighteen of the twenty-nine character-states are shared by non-proterosuchian archosaurs. A completely phenetic classification, based on overall similarity, would indeed include some other taxa in the extension of the Proterosuchia-concept, a procedure that we believe would be misleading from the evolutionary point of view.

This analysis supports the inference that characters evolved at different rates in the early evolution of archosaurs. Some characters changed in state within the group Proterosuchia itself, as reflected by all characters in the *SN* set. In both cases of *SN* character-states, we are dealing with very primitive reptilian heritages, hardly to be considered of positive selective value at the archosaurian level of evolution, and their persistence should have been disadvantageous for the changes that the proterosuchians developed in skull architecture and locomotor improvements. Other characters changed only little beyond the proterosuchian threshold; they are our *AS* set. As in the former case, these are also primitive characters, most of which are maintained in some families of primitive pseudosuchians, in the first crocodiles, or in the phytosaurs, and only exceptionally in more advanced archosaurs. They seem to indicate that the achievement of a progressive archosaurian stage was, for more than half of the characters involved, a process of gradual evolutionary change. There are also those characters of our *SS* set that changed both within the proterosuchians and beyond them. They have the combined meaning of both the previous cases, and indicate that some proterosuchians evolved beyond the level reached by some of their first derivatives. These characters are useful, indeed, to infer phylogenies: no proterosuchian descendant can be supposed to have evolved from a proterosuchian ancestor that had evolved a different state in a character belonging to the *SS* class, if it maintains the same character in the state described in that class. There remains, finally, a set of characters that show little or no change within the Proterosuchia, but that behave differently beyond the proterosuchian threshold (the *AN* class). Nine of the twenty-nine analyzed belong to this group. In most of the cases, the change in these characters in proterosuchian descendants may be interpreted as improvements linked with the emergence of new evolutionary possibilities, as we will attempt to demonstrate below.

The general pattern of character-state changes within and beyond the proterosuchians is obviously indicative of the process known as mosaic evolution (de Beer, 1954), heterobathmy of characters (Takhtajian, 1959), or stepwise evolution (Bock, 1965 presents an illuminating analysis of the process).

As a matter of fact, characters involved in mosaic evolution do not afford any basis for a clear-cut distinction of a taxon from its close descendent relatives. In our case, this is especially obvious for the characters belonging to the *SN*, *AS*, and *SS* sets of character-states. On the other hand, character-states of the *AN* class actually do afford a clear-cut distinction of the Proterosuchia from the Pseudosuchia, the Crocodilia, the Parasuchia, and the other more advanced archosaurian groups. An Aristotelian-minded taxonomist would very easily find the clue for what in the context of his philosophy should be a mere pseudoproblem: he would choose only the *AN* character-states as the sufficient and necessary features that determine the "essence" of the Proterosuchia. This procedure will not satisfy the purposes of evolutionary taxonomy, as in this universe of discourse

we are not trying to grasp the essence of any static entity, but to discover how to evaluate evolving characters in order to define evolving entities.

As far as the characters belonging to the *SN, AS,* and *SS* classes are concerned, the question could be raised whether they are not better excluded from the definition of the intension of the Proterosuchia-concept, as they are either shared by other non-proterosuchian archosaurs or not shared by all the proterosuchians. It could also be questioned whether the very existence of this kind of character-state is not an indication that the proterosuchian-concept is an artificial construct without any real referent in the objective world. We think that the answer to both questions must be negative, but in any case, it is true that we are facing a common and one of the most difficult of taxonomic problems: namely that of tracing borderlines (needed because of the requirements of taxonomy, but also, alas, because the human brain does not seem to be capable of functioning without categorizing) in ancestor-descendant series that evolve gradually from one state to the other. From the point of view of the logic of the system, an analysis of the "core" and the "fringe" of the taxonomic set represented by the proterosuchian-concept (as these terms have been defined and used by J. H. Woodger, 1952) would indeed help very much in a full elucidation of this problem. Such a sophisticated formal treatment is, however, beyond the aim of the present essay. We must keep in mind only that a fringe of vagueness seems to be unavoidable in any concept having evolving entities as referents; the peculiarities involved in such a vagueness are not to be excluded from the definition of this concept, if they are relevant for an adequate understanding of the evolutionary meaning of the entity we are dealing with. The polythetic nature of the proterosuchian-concept, with its fringe of vagueness, must be considered, on the contrary, an inherent quality of the concept, one which affords plenty of information for a better understanding of the features of early archosaurian evolution, a point which we will attempt to stress in the following part of this article.

But we must first refer to the following point: we have already said that Simpson and Gisin stressed the importance of alleged discontinuities arising during the process of detachment of a new taxon (as it shifts into a new adaptive zone) for the task of establishing non-arbitrary limits between major taxa. In Gisin's terms: "Um auch hier 'natürliche' Einheiten zu erhalten, müssen deren Grenzen den in der Natur objektiv gegebenen Diskontinuitäten, und diese einer bestimmten Qualität entsprechen" (Gisin, 1964: 9). These discontinuities given objectively in nature are believed to be the result of the threshold transition arising from a faster evolution between two major adaptive zones, a situation in which selective pressures act upon one character or a set of characters very strongly, making them evolve at a faster speed (the quantum effect). Should the explanation be correct, we would have a clue with which to trace borderlines between a series of ancestor-descendant major taxa, provided that we are able to discover which are the relevant characters involved in such a threshold effect, i.e., the "key innovations" responsible for the emergence of a new taxon. Whatever the relativity of the discontinuity, it should be possible to discover these characters if we have a complete enough fossil record.

The situation is perhaps less simple, however. Bock (1965) has contended that to postulate that in the origin of a major taxon (and hence in its delimitation) the operating process is a single-phase change, involving a switch from one major adaptive zone to another, implies an oversimplification not supported by any positive evidence. For him, the process is better thought of as a stepwise one, through which minor radiations occurred in the transitional adaptive zone. Key innovations

and preadaptations are involved in this process, but there is no special reason to assume that evolution is greatly speeded up in the intermediate area. The stepwise character of the transition between major taxa is exemplified for Bock by the mosaic pattern of character changes occurring in the known cases of the emergence of major taxonomic groups. This view seems to discourage any attempt to look for natural boundaries between major taxa and, hence, to get an accurate assessment of the intension of their concepts.

It should be very interesting, therefore, to investigate just how the evidence from early archosaur evolution does match each of these views. But such an investigation will require, first of all, a new evaluation of the evidence, for the assessment we have made of the proterosuchian character-states will have new consequences for the explanation of the origin and early evolution of archosaurs. However, before discussing our main topic, we must refer to the origin of the proterosuchians, and to the proterosuchian descendants.

THE ORIGIN OF THE PROTEROSUCHIA

Obviously, if the Proterosuchia are the first and the most primitive archosaurs, the problem of the origin of the Proterosuchia is to be identified with the problem of the origin of the Archosauria. The latter has been considered a difficult matter and has been generally approached in a very broad context, usually in connection with the discussion of the alleged early split of the reptiles into two main branches, the Sauropsida and the Theropsida. A special account of this general question is beyond our present aim and we must restrict ourselves to the points more closely connected with archosaur ancestry [for a general survey of the whole matter, see Vaughn (1955), Watson (1954, 1957), Parrington (1958), Tatarinov (1959), Olson (1962)].

The fact that archosaurs and lepidosaurs have two-arched skulls led to their being grouped in one single taxon, the Diapsida, in early classifications. This taxon-concept has been generally abandoned since Romer (1956) advanced the current classification. But the general idea of a close relationship between archosaurs and lepidosaurs survives, and the concept of Diapsida is frequently used in phylogenetic discourse, although devoid of any explicit taxonomic intention. How close this relationship is is a matter of the disagreement, but little doubt has been cast upon the assumption that the two groups had a common origin, or that archosaurs are derived from early lepidosaurians.

The critical groups for the enquiry into archosaurian ancestry usually have been considered to be: the younginid eosuchians, the millerettiforms, and the captorhinomorph cotylosaurs. As far as the different possible hypotheses of archosaurian ancestry are connected with these three groups, we can speak of the younginid hypothesis, the millerettiform hypothesis, and the captorhinomorph hypothesis.

In a recent paper (Reig, 1967), I have briefly discussed these different hypotheses, pointing out that the proterosuchian character-states make it necessary to rule out both the younginid and the millerettiform hypotheses. Each of these groups is more advanced than the first archosaurs (the proterosuchians) in relevant character-states.

The younginid hypothesis was first advanced by Broom (1914, 1922, 1924a, 1946) and has been subsequently adopted by such authors as Camp (1945), Piveteau (1955) and von Huene (1956). This hypothesis maintains that the archosaurs, the rhynchocephalians, and the squamates took their origin from the younginids, represented by the small South African *Cistecephalus* Zone reptiles *Youngina*, *Youngoides*, and *Youngopsis*, known mostly from skull material. The family Younginidae forms the central group of the suborder Younginiformes of the Lepidosauria in Romer's (1956) classification, the other

families of the same suborder being Paliguanidae, Prolacertidae, and Tangasauridae. The younginids have both the diapsidan temporal opening fully developed (character-state i of our *AA* class) and the typical lepidosaurian otic notch, formed by a curved posterior border of the quadrate and defined above by a small spur of the squamosal (in disagreement with our proterosuchian character-state 4). At the same time, the suspensorium is nearly at the same level with the occipital region (contradicting our character-state 6), and the quadrate is attached by suture with the squamosal in a monimostylic way (in contrast with character-state vi of our *AA* class).

It is now generally accepted that the younginids can be considered as the stem group of the Rhynchocephalia and that the origin of the Squamata is better sought in the Prolacertidae (Camp, 1945; Parrington 1935; Kuhn-Schnyder, 1954, 1962). As far as the archosaurs are concerned, the younginid ancestry has been seriously questioned by Romer (1946, 1956). And apart from the arguments of this author, it is clear that the younginids cannot be considered ancestors of the proterosuchians because of the structure of the quadrate, as even the first proterosuchians (i.e., *Chasmatosaurus*, Brink, 1955) show a movable quadrate, articulated with the squamosal through a head, a condition which has been established in the millerettids (Watson, 1957). But in addition, the lack of any sort of otic notch and the very backward position of the mandibular articulation of the quadrate (shown already in the most primitive proterosuchians) definitely preclude the idea of any kind of younginiform ancestry for them. The proterosuchian character-states 4 and 6 constitute a serious objection to the younginid hypothesis, and this is better abandoned.

The core of the Millerettiformes (also a suborder of the Eosuchia of the Lepidosauria in Romer's classification of 1956) is formed by several genera described by Broom (1938, 1940, 1948) from the same *Cistecephalus* beds of South Africa and placed in the family Millerettidae. Earlier genera of the same group are usually referred to different families. The whole taxon has been carefully surveyed by Watson (1957) who maintained that these are sauropsid reptiles possessing very primitive qualities, though not having already developed the two-arched condition. He suggested (1957: 388) that the thecodonts could have come direct from the Millerettiformes (called by him Millerosauria), and, in the chart of figure 23 of the same work, he derives the Pseudosuchia plus later archosaurs and the "Erythrosuchia" (= Proterosuchia), as a separate branch, from the "millerosaurs." The implication is that the proterosuchians do not belong in the ancestry of later archosaurs (a contention not expressed in his text), but that both pseudosuchians and proterosuchians evolved independently from "millerosaurs." As we shall make more evident below, no relevant evidence exists ruling out the proterosuchians from the ancestry of the pseudosuchians and, on the contrary, the presence of such intermediate forms as *Euparkeria* suggests that proterosuchians actually were the ancestors of the pseudosuchians.

As far as proterosuchian origin from the millerettids is concerned, it is highly improbable that at least any of the small genera of the *Cistecephalus* Zone could be in the line of proterosuchians. All of them have an otic notch already developed, and the quadrate in an upright position, with the mandibular articulation close to the occipital plane. These are character-states that are not expected to be found in any proterosuchian ancestor. It is true that the millerettids are more plausible archosaur ancestors than are the younginids, because the former have a movable quadrate-squamosal articulation, but, at the same time, the millerettids had not reached the diapsid condition already developed in the young-

inids. Furthermore, the millerettids could hardly be considered as adequate forerunners of the contemporaneous *Archosaurus* from the Russian Upper Permian Zone IV. This genus indicates that, at the time the millerettids thrived, the proterosuchids were fairly large animals which had already developed their typical character-states.

However, discarding the millerettids as direct proterosuchian ancestors is not the same as discarding the millerettiform hypothesis, since the group is not restricted to millerettids of the South African *Cistecephalus* Zone. The older *Tapinocephalus* Zone of the Karroo succession has yielded *Broomia*, a genus tentatively placed in a family of its own, and the still older strata of the Mesen River in Russia (Upper Kazanian, Zone II of the Russian Permian) afforded *Mesenosaurus*, a genus considered of pelycosaur affinity by Efremov (1938) and by Romer and Price (1940), but more correctly placed in the Millerettiformes as the type of a family of its own (Watson, 1957; Romer, 1956; Tatarinov, 1964). Romer (1967) has stressed the phylogenetic importance of the Millerettiformes. They are likely to have been a widespread group, both in time and in space. Can it be supposed, therefore, that the Proterosuchia evolved from some early millerettiform population? This is hardly probable, as such an early member of this taxon as *Mesenosaurus* had already acquired, according to published descriptions, a perfect otic notch. The Millerettiformes are better considered as forerunners of the Lepidosauria, not as a group having direct relationships with the archosaurs.

Romer (1956: 519) suggested that the archosaurs might have arisen independently from cotylosaur ancestors. It is obvious that the captorhinomorphs are here implied, as he did not consider other cotylosaur groups as being close to the archosaurs. The two-arched temporal region of archosaurs and lepidosaurs would in this view be another case of parallelism, which, by the way, might also be the case if one advocated a millerettiform ancestry.

The first adequately known captorhinomorph, and also the earliest adequately known reptile, comes from the Lower Pennsylvanian (Westphalian A) of the Port Hood formation in Nova Scotia. This is the genus *Romeriscus*, a limnoscelid recently reported by Baird and Carroll (1967). Remains of two romeriid captorhinomorphs and one pelycosaur have also been described from the Joggins of Nova Scotia, a slightly higher level in the Lower Pennsylvanian (Westphalian B) (Carroll, 1964). Romeriids are represented also by dubious remains from the Middle Pennsylvanian, and they are better known through their last representatives in the Lower Permian (*Romeria*, *Protorothyris*). The other captorhinomorph family, namely the captorhinids, has its first members in the Lower Permian Leonardian stage (see Table I), with *Captorhinus* as a well-known representative. Members of this family are, moreover, the latest captorhinomorphs, reaching the early Guadalupean and early Kazanian (*Rothia*, *Kahneria*, etc.). The limnoscelids departed very early from the main line of reptilian evolution (Baird and Carroll, 1967), so that only romeriids and captorhinids could be relevant in the discussion of archosaur ancestry.

It is clear that both romeriids and captorhinids would make better archosaur ancestors than younginids, prolacertids, or millerettids, in the sense that they do not contradict the requirement of the absence of an otic notch as demanded by the proterosuchians. They are, however, very archaic, fully anapsid, and with the suspensorium not primarily posterior in position. The form and the relationships of the quadrate, moreover, are more archosaur-like in the millerettids than in the captorhinomorphs. However, Parrington (1958) has demonstrated that the millerettid condition of the quadrate is easily derived from that of *Captorhinus*. But, as the same arguments used by Parrington

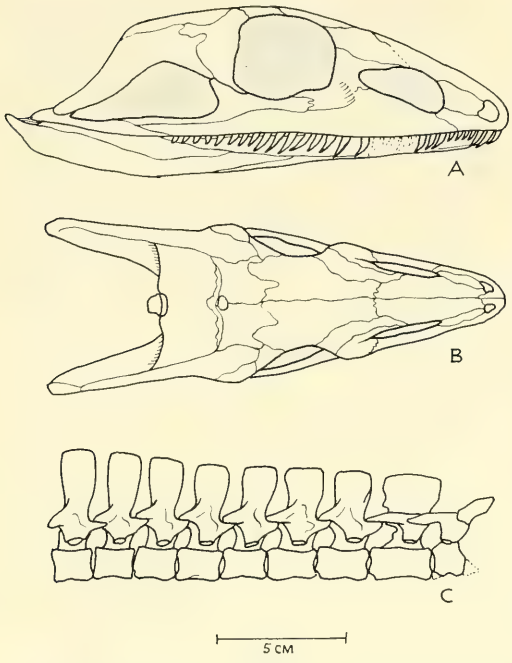

Figure 6. *Varanodon agilis* Olson. A, lateral view of the skull; B, dorsal view of the skull; C, series of cervical vertebrae. (From Olson.)

could be applied to derive the archosaurian condition of the quadrate from that of the captorhinids, this does not run counter to the possibility of captorhinomorph derivation of the archosaurian skull. In fact, no theoretical objection can be raised against the contention that the proterosuchian skull, diapsid, without otic notch, and with a very posterior suspensorium could be derived from a romeriid or captorhinid skull. Furthermore, the postcranial skeleton is so primitive in these cotylosaurs that practically every proterosuchian character-state of that part of the body could easily be thought of as having evolved from a captorhinomorph state.

But it is clear that too large a morphological gap exists between even the more primitive proterosuchians and the more advanced captorhinomorphs, and neither romeriids nor captorhinids show any definite trend towards some of the peculiar archosaurian character-states. Even if intermediate forms should be discovered between captorhinomorphs and early archosaurs, the amount of difference between the ancestor and the descendent groups would necessarily be so great that the linking group might better be considered as a major taxon of its own. In this case, the captorhinomorph hypothesis should be transformed into one arguing for ancestry from this intermediate taxon.

Another objection to the captorhinomorph hypothesis is the lack of explanatory value, as it can be agreed that many reptilian groups could eventually have stemmed from captorhinids or romeriids. Moreover, it becomes clear that this hypothesis should be abandoned if another reptilian group more closely related to the first archosaurs exists. As I have already proposed (Reig, 1967), I believe that a strong case exists for assigning this role to a definite group of pelycosaurs; this makes it necessary to put forward a new hypothesis, namely the pelycosaurian hypothesis.

This idea is not completely new. The notion of pelycosaur and archosaur relationships was first expressed by von Huene (1911), when he discussed the position of *Erythrosuchus*. He found that this genus shared with pelycosaurs so many features in skull and postcranial morphology, that he created for it an order of its own, Pelycosimia, a name coined with the evident purpose of expressing the idea of pelycosaur relationships. He later abandoned the idea of the Pelycosimia as a separate order, and the name has been used in its original spelling, or as Pelycosimioidea, as an equivalent of Proterosuchia, or Proterosuchoidea, and, hence, as a taxon subordinated in the Thecodontia.

More recently, Rozhdestvenskii (1964: 204) suggested plainly the pelycosaur origin of the archosaurs, when he said: "The mammal-like reptiles, and particularly the pelycosaurs, are also to be considered as archosaur ancestors. The earliest archosaurs, the Triassic thecodonts, are

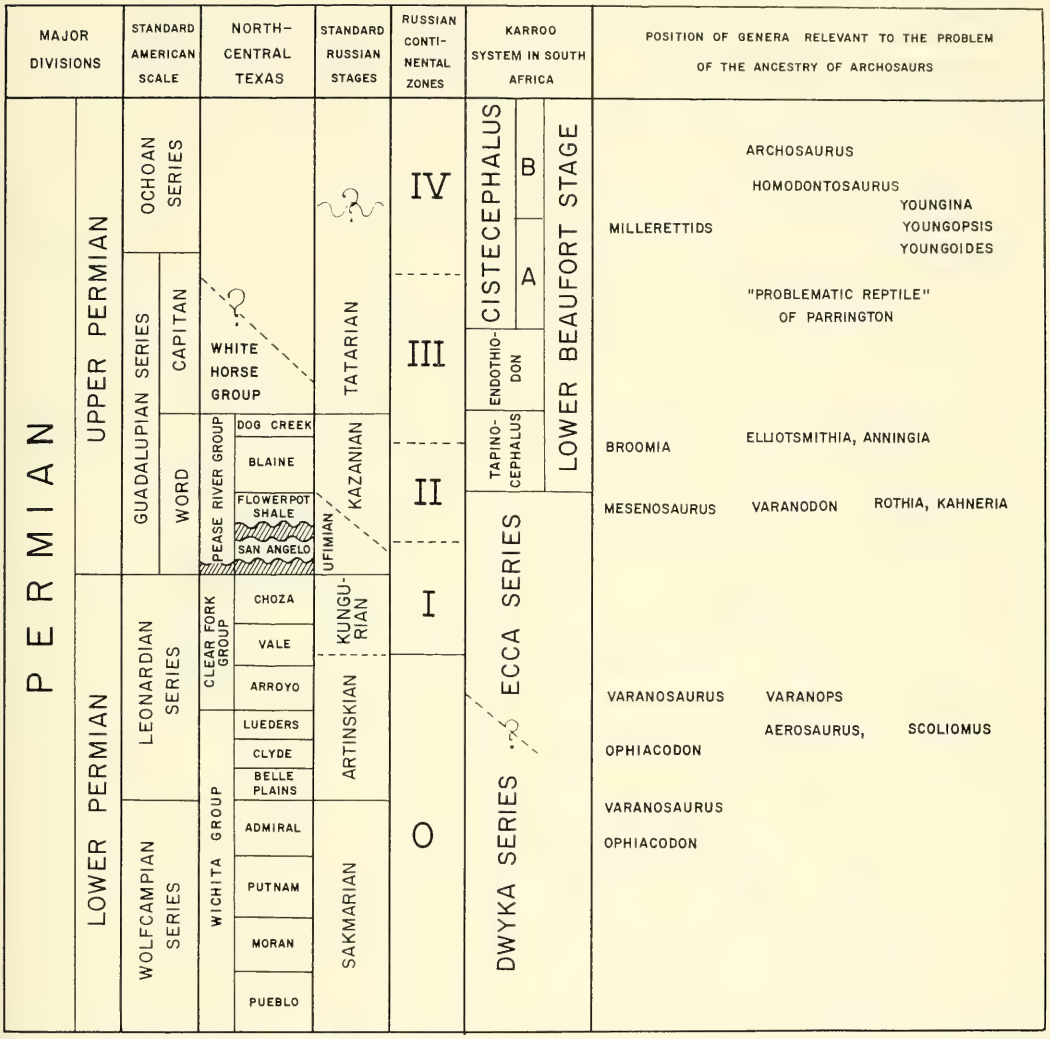

TABLE I. CORRELATION CHART OF THE VARIOUS DIVISIONS OF THE PERMIAN IN U.S.A., SOUTH AFRICA, AND RUSSIA. (MAINLY FROM DUNBAR AND FROM OLSON.)

significantly similar to the pelycosaurs, both in general features and in details."

The pelycosaurs are, however, a large group including several specialized subordinate taxa that are surely not connected with the archosaurs. The more generalized members of this order are to be sought in the Ophiacodontia and in the Varanopsidae among the Sphenacodontia. Even though some ophiacodontids show several notable resemblances to the more primitive proterosuchians, this is not the group most likely to include the archosaur ancestors. It is the varanopsids that have features that strongly suggest proterosuchian relationships, and that have developed some character-states that are found elsewhere only in the archosaurs among the reptiles. Olson (1965) has recently described *Varanodon agilis* (Fig. 6), an advanced varanopsid

from the Guadalupean of Oklahoma, which strongly suggests a theoretical proterosuchid ancestor in skull and postcranial structure. It is thus desirable to consider the composition of this family.

The best known genus of the Varanopsidae is *Varanops*, from the Clear Fork beds of Texas (Leonardian, Lower Permian: see Table I to visualize the Permian successions), carefully described by Romer and Price (1940). These authors referred to the same family the genera *Aerosaurus* and *Scoliomus*, from the largely equivalent Abo beds of New Mexico, the South African *Elliotsmithia* and *Anningia* (= *Galesphyrus*) from the *Tapinocephalus* Zone of the Upper Permian, and the Russian *Mesenosaurus*, which, as has already been said, is now better placed in the Millerettiformes. *Homodontosaurus* of the South African *Cistecephalus* Zone has also been included in the same family. However, the position of the South African and New Mexican genera is doubtful. Watson (1957) suggested that *Elliotsmithia* and *Anningia* might be considered to be millerettids; *Aerosaurus* and *Scoliomus* are known from material too fragmentary to permit an accurate family allocation. *Homodontosaurus*, a pelycosaur according to Broom (1949), is considered a therapsid by Brink (1950), and the nature of the material suggests that it is better considered as a synapsid *incertae sedis*. Olson (1965) maintains that *Varanops* and his new genus *Varanodon* (Fig. 6) are the only genera to be considered as certainly belonging to this family, and, as far as the other genera are concerned, in his view *Elliotsmithia* is the only one for which a convincing case can be made.

Extending from the lowest Vale (*Varanops*) to the *Tapinocephalus* Zone, the family Varanopsidae would be a long-lived one during Permian times, and its extension in time matches very well that which would be expected for a group ancestral to the archosaurs.

The skulls of varanopsids and ophiacodonts share a number of characters with the proterosuchians. First of all, the absence of an otic notch, the presence of a lateral temporal fenestra, and the posteriorly situated suspensorium with the quadrate strongly slanting backwards, constitute an assemblage of characters that we have not found associated in any of the other groups alleged to be connected with archosaur ancestry; by themselves these make a strong case for suggesting relationships. Besides this, there is the common possession of postparietal and postfrontal bones and of a pineal foramen, conditions that even though not indicative of special relationships, for the same character-states are shared by other primitive reptiles, do not contradict our hypothesis. Far more important is the fact that so typical an archosaur character-state as the presence of an antorbital fenestra has been described in *Varanodon* and is apparently also present in *Varanops* (Olson, 1965). At the same time, the characteristic archosaur mandibular fenestra is found well developed in *Ophiacodon* (Romer and Price, 1940) and apparently also in *Varanops* (a detailed account of the mandible of *Varanodon* has not yet been reported). Moreover, ophiacodontids and varanopsids share with the proterosuchians an elongated antorbital region, an occipital plane that is concave and slants forward towards the skull table (as in most pelycosaurs), and large prefrontal bones that project laterally and form a ridge, making an abrupt limit between the roof of the skull in front of the orbits and the lateral antorbital region. The palate is not adequately known in the Varanopsidae, but typical proterosuchian character-states, such as pterygoid flanges, teeth on these flanges, and long and narrow interpterygoid vacuities, are observable in *Ophiacodon*. Pelycosaurs also have in common with the proterosuchians and some later archosaurs the presence of epipterygoids and the small size of the posttemporal fenestra, and in both groups the prootics are extensive. A peculiar condition of the

pelycosaurs is the presence of a prominent *dorsum sellae* formed mainly by the prootics, rather than by the basisphenoid (Romer and Price, 1940; Romer, 1956). This condition is not known in the proterosuchians, but the fact that in the phytosaurs the *dorsum sellae* is partly formed by the median union of the prootics (Camp, 1930), suggests that participation of the prootics in the *dorsum sellae* is to be expected in proterosuchians.

The proterosuchian skull is metakinetic (Versluys, 1910: 197), and this seems also to be the original condition of the pelycosaurs (Versluys, 1912: 661). As far as skull kinetism is concerned, however, an important difference between the pelycosaurs as a whole and the proterosuchians is the nature of the quadrate, which is completely monimostylic in the former and streptostylic in the latter. It is clear, nevertheless, that more research is needed in order to know which is the primitive condition of this character. We have already mentioned that the movable quadrate of the millerettids seems to be easily derivable from the rigid condition of *Captorhinus* (Parrington, 1958).

Additional differences are shown in the fact that all pelycosaurs lack the upper temporal fenestra and that they retain the tabular and supratemporal bones and have not developed laterosphenoid ossifications. All these character-states are, however, to be expected in proterosuchian ancestors, the different state in the first archosaurs being obviously an evolution from a primitive condition like that seen in the pelycosaurs or romeriid captorhinomorphs. Romer and Price (1940: 194–195) argued that the diapsid condition of the archosaurian skull is hardly derivable from the synapsid condition of the pelycosaurs. Their arguments, however, do not seem to the present author very convincing, and there seems to be no serious doubt that, as Kuhn-Schnyder recently advocated (1962), the development of the lower temporal fenestra is the first step towards the realization of the two-arched, diapsid condition. The size and position of the temporal fenestra in the Varanopsidae make it clear that this fenestra is homologous with the diapsidan lower temporal fenestra. Another point against pelycosaur-archosaur relationships in the Romer and Price argument, the morphology of the pelycosaur occiput, is contested by present knowledge of occipital structure in the proterosuchians.

Another distinction refers to the anterior extensions of the lacrimals that in ophiacodontids and varanopsids contribute to the borders of the external nares. This feature is not shown by any proterosuchian, but the fact that the same condition is observed in other primitive groups, such as millerettids, diadectids, gephyrostegids, and captorhinomorphs, suggests that this is a primitive reptilian heritage; it is not surprising to find it in proterosuchian ancestors.

Taking into account the combined group of the ophiacodonts and varanopsids, it is highly suggestive that they share four of the eight character-states of *AA* class (2, 3, 5, 8) that refer to skull characters, and that in one other (1) they are intermediate. Even more suggestive is the fact that they share all the thirteen skull character-states of the proterosuchians (character-states 1–13 of our list). In short, the data of skull anatomy seem to indicate that the primitive pelycosaurs of the ophiacodontid-varanopsid group make better proterosuchian (and archosaur) ancestors than any other reptilian group. Among these, the Varanopsidae show character-states suggesting that they are close to the group from which the proterosuchians may have arisen, as they have already developed the otherwise characteristically archosaurian antorbital fenestra and have a very large lateral temporal opening and strongly backward-oriented suspensorium.

The same conclusion is supported by the axial skeleton. The pelycosaurian vertebral column is of course more primitive

than the proterosuchian one, as the vertebrae have persistently notochordal centra, intercentra commonly present in all the presacral vertebrae, and a presacral number of twenty-seven. The vertebral morphology, however, does not preclude archosaur ancestry in any way. On the contrary, proterosuchian vertebrae show character-states such as the presence of lamellae connecting the apophyses for the rib heads (present also in ophiacodonts, at least) that seem to be reminiscent of the primitive pelycosaur condition. The atlas-axis complex is closely comparable in *Chasmatosaurus* and the ophiacodonts, as Broili and Schroeder have already pointed out (1934), and the Varanopsidae (Fig. 6c) add to the general picture the fact that they have, as in the primitive proterosuchians, elongated cervical centra (Romer and Price, 1940: 274; Olson, 1965: 53) and a tendency for the dorsal rib facets to become more closely approximated from the front backwards. The similarity in sacral vertebrae is also striking, as von Huene (1911: 36) noted, and this similarity becomes more evident when primitive pelycosaurs are considered, as both ophiacodontids and varanopsids have only two sacral ribs. Mention should also be made here of the few vertebrae associated with portions of humerus and ulna and other fragments that Parrington (1956) described from the Upper Permian (*Endothiodon* Zone) of Tanganyika. The vertebrae of this "problematic reptile" are suggestive of a transitional type between pelycosaur and archosaur vertebrae; they are pelycosaurian in the retention of the notochordal canal, and archosaurian in the form and position of rib articulations. It is of interest to note that these remains come from a level in the Upper Permian immediately following the *Tapinocephalus* Zone, which yielded the specimens of the supposed last varanopsid, *Elliotsmithia.*

Of prime interest for the pelycosaur hypothesis are the striking resemblances that exist in the morphology of the appendicular skeleton between proterosuchians, on the one hand, and ophiacodontids and varanopsids, on the other. Members of both these pelycosaurian families show the primitive reptilian feature of sprawled legs, as in the proterosuchians (character-state 16), and both are, of course, quadrupedal (character-state 15). But, at the same time, ophiacodontids and varanopsids present the characteristic archosaurian limb disparity (character-state xiii of the *AA* class) in just the stage of development shown by the proterosuchians (character-state 17). The girdles and the limbs show striking points of affinity, even in details. The scapular blade in *Chasmatosaurus* and *Cuyosuchus* is closely comparable to that in *Ophiacodon* and *Varanops*: short and broad by archosaurian standards, with a supraglenoid buttress and a supraglenoid foramen (at least in *Cuyosuchus*) (Fig. 7). This character-state (27) is not shared by all proterosuchians, as has already been said, and it is interesting that such a feature of the *SN* class should be shared by varanopsids and ophiacodontids. As far as the coracoids are concerned, pelycosaurs differ strongly from archosaurs in the possession of two coracoidal ossifications, a point that has been stressed by Romer and Price (1940: 194) in discarding the possibility of pelycosaur-archosaur relationships. But it is now commonly agreed that the single archosaur coracoid represents the synapsid precoracoid, and the presence of two coracoids in various primitive reptiles (such as pelycosaurs, captorhinids, procolophonoids, and pareiasaurs) proves that two coracoidal ossifications are an early acquisition in the first reptiles, and that this condition has been lost in later stages of reptilian evolution, the synapsids being the only group in which it survived. From this assumption, it is logical to conclude that in the ancestors of archosaurs a trend towards the reduction or disappearance of the posterior "true" coracoid occurred. It is therefore highly significant that among the Varanopsidae, which show

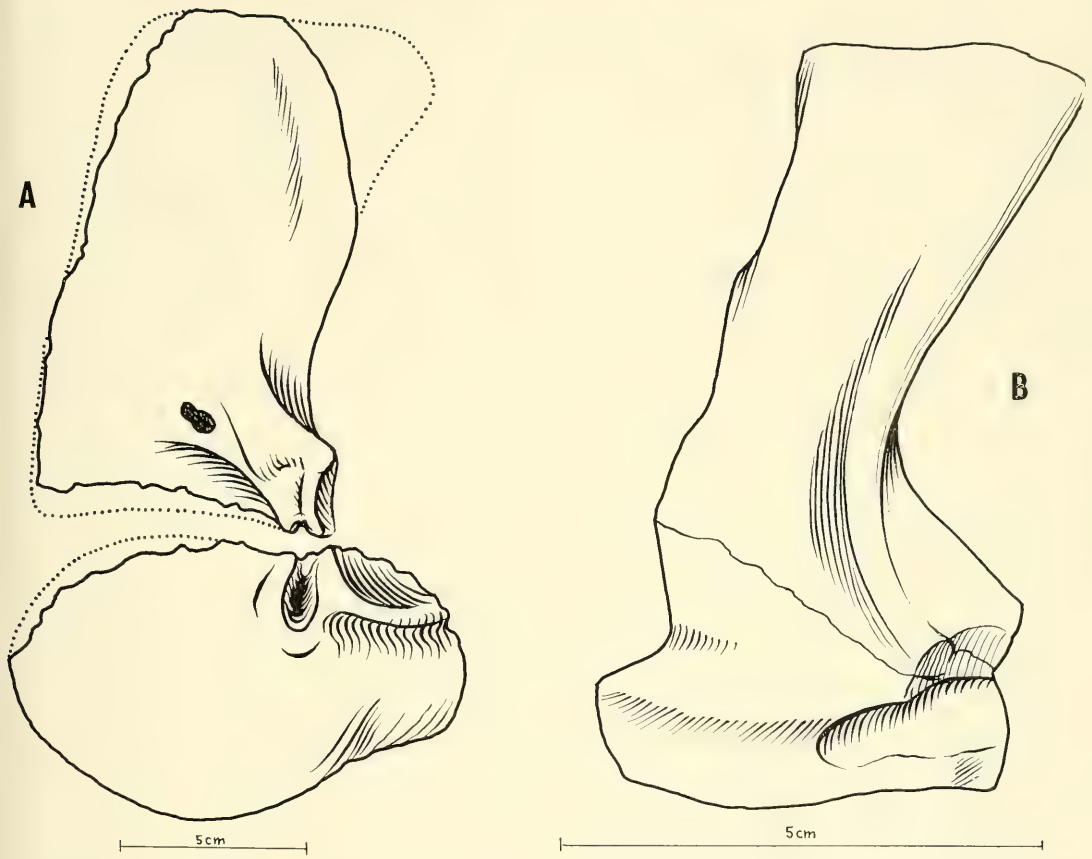

Figure 7. Scapula and coracoid of one proterosuchian and one varanopsid pelycosaur. A, *Cuyosuchus huenei* Reig; B, *Varanops brevirostris* (Williston). (A, from original specimen; B, from Romer and Price.)

so many similarities to the proterosuchians, *Varanops* (Fig. 7) is unique among pelycosaurs in lacking a posterior coracoidal ossification (Williston, 1914)—a feature that has been interpreted by Romer and Price (1940: 274) as a lag in ossification; this lag has been reported by the same authors (1940: 263) as a characteristic feature in sphenacodonts. The situation in other typical varanopsids is not clear in this respect, and the ophiacodonts exhibit the characteristic double condition of the pelycosaurian coracoids.

In pelycosaurs, the humerus is characterized by the expanded and twisted ends, the distinct shaft region, the presence of a large entepicondylar foramen, and a well-developed deltopectoral crest. The known humeri of proterosuchians, with the exception of *Cuyosuchus*, also possess expanded and twisted ends (character-state 20), a strong deltopectoral crest, and distinct shaft. They look very different from the humeri of most of the pseudosuchians and are very close to the pelycosaurian ones, but they do not show the entepicondylar foramen characteristic of the latter. However, it must be noted that the humerus of *Chasmatosaurus* recently figured by Young (1963) is not only closely comparable with that of *Varanops*, but also shows a discontinuity in the entepicondylar border in

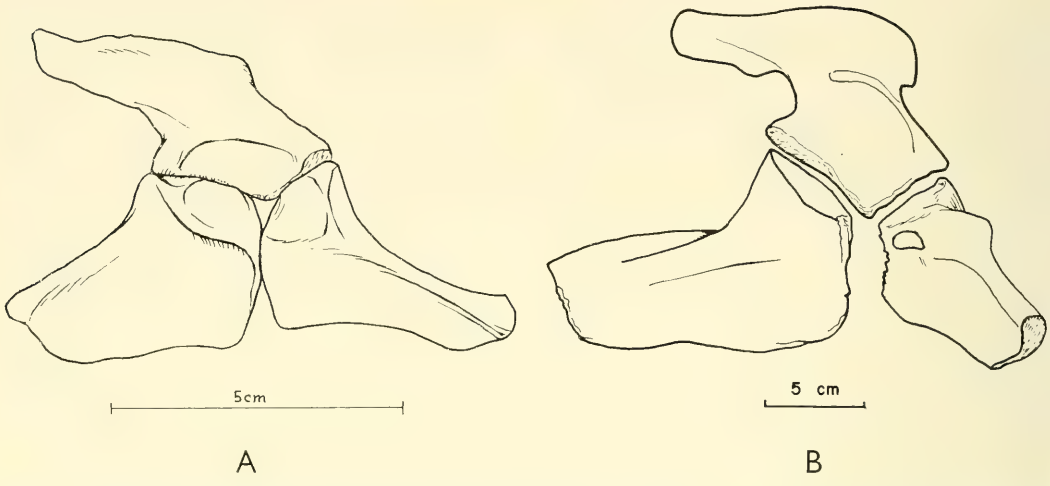

Figure 8. Pelves of one varanopsid pelycosaur and one proterosuchian thecodont. A, *Varanops brevirostris* (Williston) (from Romer and Price); B, *Vjushkovia triplicostata* von Huene (from von Huene).

the position where the entepicondylar foramen should be placed, which suggests that such a foramen might be present in this genus, its external bridge of bone being broken in the specimen. An ectepicondylar notch is also evident.

The anterior epipodials are short and subequal in size both in pelycosaurs and proterosuchians. The former have a well-developed olecranon on the ulna, which is apparently lacking in the proterosuchians. But, as Romer and Price have indicated (1940: 46), the extreme lag in ossification of the olecranon during ontogeny makes this character untrustworthy in problems of phylogeny. It is suggestive that the ulna of *Varanops* looks very much like that of *Chasmatosaurus* described and figured by Young (1936), especially as regards the proximal end, which in both is massive and has a relatively weakly developed olecranon area.

We have already said that the pelvic girdle of the primitive proterosuchians may be better described as incipiently triradiate, the triradiate condition being more evident in such advanced forms as *Erythrosuchus*. Earlier forms retain many primitive characteristics, such as a reduced but fairly continuous puboischiadic plate. The pubis in *Varanops* (Fig. 8) has a very strong upper border directed forwards and downwards, and can be described as a twisted plate of bone, as is the case in the proterosuchians. The ischium also shows a strong upper border directed backwards and downwards, and the puboischiadic plate is reduced. These features are closely comparable to those in primitive proterosuchians and suggests that the archosaurian trend toward a triradiate pelvis was beginning to develop in *Varanops*-like pelycosaurs. This corresponds to our proterosuchian character-state 25. As far as the other pelvic characters are concerned, the ilia of *Chasmatosaurus* and *Shansisuchus* are very like that of *Varanops* in that the anterior process of the blade is very weakly developed (character-state 22). This process is absent in the ophiacodonts, but is very well developed in later sphenacodonts and edaphosaurs. The posterior spine of the blade is long and narrow in ophiacodonts and more proterosuchian-like in *Varanops*. In short, the ilia of varanopsids and proterosuchians are very similar, which is not the case in more advanced pelycosaurs.

The femur of proterosuchians has been reported as being very primitive in that it possesses a terminal head, an intertrochanteric fossa, and an internal trochanter (character-states 18, 19). These features are characteristically present in the pelycosaurs. In pelycosaurs, however, the posterior condyle is far larger than the anterior one, as is clearly shown in advanced sphenacodonts and in edaphosaurs. In the proterosuchians, this characteristic is not noticeable, and it is again strongly significant that this condylar disparity is far less marked in *Varanops* and in the ophiacodontid *Varanosaurus* than in the typical pelycosaurs. The femur of *Chasmatosaurus* figured by Young (1963) looks very like that of *Varanops* in this respect and also in general shape.

The posterior epipodials are generalized in both pelycosaurs and proterosuchians, and do not afford any evidence of relationships. As far as the foot is concerned, in both groups the astragalus and calcaneum are large elements, closely appressed one to the other and to the fibula and tibia, so that most of the ankle joint is mesotarsal (character-state 21). In addition, the metatarsals of *Chasmatosaurus* (Young, 1936, fig. 12) are very like those of *Varanosaurus* and *Varanops* in general shape and proportions. In the three genera, the fourth metatarsal is the largest, and the size progression is the same: 1<2<5<3<4. The phalangeal formula of *Chasmatosaurus*, as restored by Young, is, as in pelycosaurs, the primitive reptilian one, with the improbable exception of the three phalanges of the first toe, which is almost surely a faulty reconstruction.

We should finally mention that an additional point of resemblance is afforded by the dichocephalous type of ribs, a characteristic archosaur feature (character-state x of our *AA* class) that is shared by ophiacodontids, varanopsids, and most of the other pelycosaurian groups, and that pelycosaurs also agree with the proterosuchians in the presence of a dermal pectoral girdle (character-state 28) and the absence of dermal armor (character-state 29).

As in the case of the skull characters, an analysis of the traits of the postcranial skeleton affords an overwhelming array of similarities between the proterosuchians and the ophiacodontid-varanopsid group. Both groups share three of the five character-states of our *AA* class and practically the whole set of the sixteen postcranial character-states we have listed for the proterosuchians. Obviously, these figures could be misleading, as they do not cover important dissimilarities that we have pointed out in the text. But, as we have already discussed, these dissimilarities do not preclude in any case the possibility of the pelycosaur hypothesis, the proterosuchian state of the pertinent characters being readily derivable from the pelycosaurian state. What they indicate is that the group of pelycosaurs in question has not reached the proterosuchian stage of evolution in several relevant features, a conclusion that does not contradict our hypothesis, since it is not here intended to demonstrate that these pelycosaurs *are* proterosuchians, but only that they include the taxon from which the proterosuchians could have taken their origin.

As in the case of the skull characters, we have also observed that within the ophiacodontid-varanopsid group of pelycosaurs, the Varanopsidae seem to be plainly in the line of archosaur ancestry, as they have already developed, or begun to exhibit, relevant trends toward the first archosaurs, such as the single nature of the coracoid, the general shape of the pelvis, the elongated cervical centra, and the pattern of the rib facet displacement in the dorsal vertebrae. None of these trends is developed in more advanced pelycosaurs, and when we also recall that the archosaurian features already developed in the varanopsid skull, such as the antorbital fenestra, the large lower temporal opening, the probable presence of a mandibular fenestra and the backward displacement of

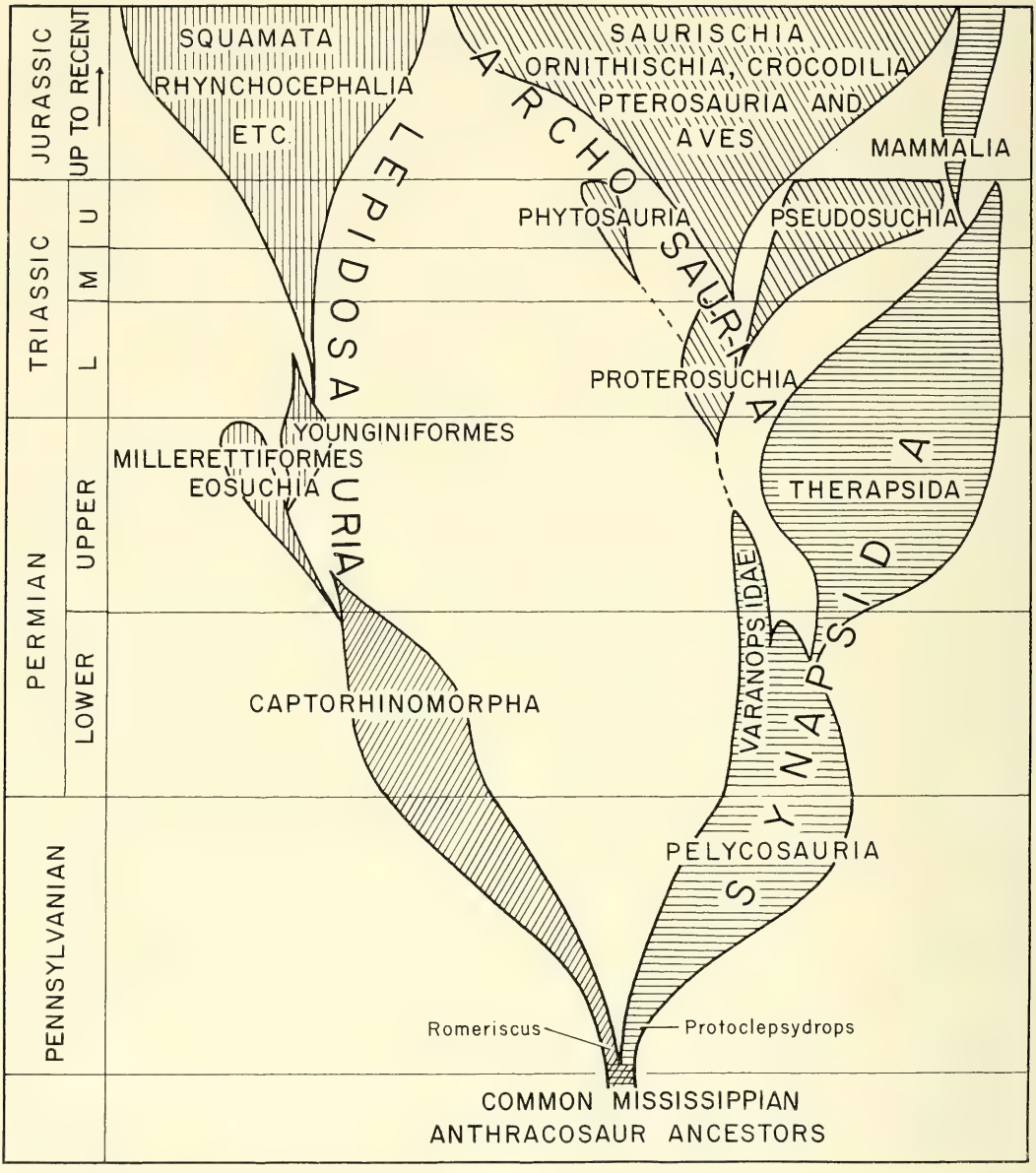

Figure 9. Phylogenetic diagram of the suggested ancestry of the Archosauria and the probable relationships among captorhinomorphs, synapsids, lepidosaurs and archosaurs. (Modified from Reig, 1967.)

the mandibular articulation, are not developed in the more advanced pelycosaurs, we can agree with Olson's suggestion that the Varanopsidae have departed from the main lines of pelycosaur evolution (Olson, 1965). Romer and Price (1940), however, maintained that the Varanopsidae are ancestral sphenacodontians, a contention that does not seem to be supported by the specialized, archosaur-like features shown by the known members of this family. The occurrence of true sphenacodonts as early

as the Lower Pennsylvanian (Carroll, 1964; Baird and Carroll, 1967) clearly indicates, moreover, that the hypothesis of derivation of sphenacodontids from varanopsids should be at least submitted to a critical reappraisal. In our present state of knowledge, I think it is more reasonable to place the Varanopsidae in the Ophiacodontia, as a family in which at least the known members separated from the main direction of synapsid evolution to follow their own evolutionary course, a course that eventually led to their transformation into the proterosuchians. The possibility should not be discarded, however, that very early, unknown varanopsids could be the common ancestors of both sphenacodontians and proterosuchians.

Mention must also be made here of the problematic late Pennsylvanian reptile *Petrolacosaurus* (Peabody, 1952). On the basis of strong similarities in the palatal structure with the eosuchian *Youngoides* and rather less relevant postcranial features, Peabody interpreted this genus as being a primitive eosuchian and proposed a diapsid reconstruction of its skull. This reconstruction is obviously quite hypothetical, but the material seems to suggest, at least, that it possessed a lower temporal opening. Analyzing the quadrate region of the skull and other cranial features, Watson (1954) contended that *Petrolacosaurus* is to be considered a theropsid reptile, a contention that Vaughn (1955) is inclined to accept. In agreement with these views, Romer (1966b) places *Petrolacosaurus* as a probable member of the primitive edaphosaurian family Nitosauridae. It seems to me highly probable that this genus belongs to the Pelycosauria, the data afforded by Peabody giving strong support to this interpretation. If this is the case, it must be noted that the structure of the palate and the elongated cervical centra shown by *Petrolacosaurus* are character-states suggestive of archosaurian ancestry. But in other respects, this genus is so primitive that it cannot successfully contend with the known varanopsids as a proterosuchian ancestor, the geological occurrence of the varanopsids being also more consistent with the idea that they make better forebears of the archosaurs.

I believe that the body of evidence supporting the pelycosaurian hypothesis (Fig. 9) is stronger by far than that supporting any alternative view, and I have not been able to find any serious evidence against it. Apart from its empirical foundations, it can also be said that the hypothesis is also supported by such attributes as explanatory value and simplicity. It is able both to explain the until now obscure question of archosaurian origin in a simple way, and also to explain the reasons for seemingly aberrant features of the late Varanopsidae and the peculiar characteristics of the proterosuchians. It is also rich in suggestions that explain the ecological factors underlying early archosaurian evolution, and is in agreement with other cases of emergence of major groups, namely a pattern of steady development of features of the evolving group.

ECOLOGICAL AND EVOLUTIONARY FEATURES WITHIN THE PROTEROSUCHIA

We have already suggested in the introduction that the proterosuchians represent the first step in an exploratory radiation performed by the thecodonts before the complete dominance of the archosaurs at the end of the Triassic. Now, it will be of prime interest to investigate what conclusions can be drawn about the pattern followed by early archosaurian evolution during this first phase. For this, knowledge of the ways of life and the ecological roles of the proterosuchians can afford important data.

Not much doubt can be cast upon the conclusion that the proterosuchids were mostly aquatic, predaceous reptiles living in ponds, lakes, and rivers, using swimming as their main form of locomotion, and preying upon other vertebrates. This con-

clusion is based on the similarity that they display in body form and proportions to modern crocodiles and in the characteristics of the skull and the dentition. Tatarinov (1961: 130) suggested that big forms like *Chasmatosaurus* fed upon fishes, and that the small forms like *Chasmatosuchus* might have been invertebrate eaters (how far invertebrates contributed to the diet of the proterosuchids is not clear). Moreover, the fact that proterosuchids have been found associated with unquestionable water dwellers, gives additional support to this conclusion. Hughes (1963: 221) affirms that in South Africa "bones of *Lystrosaurus* and *Chasmatosaurus* may be found side by side," and although Robinson (*fide* Hughes, 1963, same reference) cast doubts about the association of these two genera in the Panchet beds of India, this association, with the presence of labyrinthodonts as an additional element, has recently been reported by Satsangi (1964) in the Raniganj coal field. Moreover, Young (1936) reported the same fact in China. It must be recalled that *Lystrosaurus* is a dicynodont very specialized for an aquatic way of living, as indicated by the dorsally placed nostrils, the orbits projecting above the level of the roof of the skull, and the features of the carpus and tarsus. *Lystrosaurus* seems to have been an herbivorous animal not unlike the modern hippopotamus in habits, and its frequent association with the carnivorous *Chasmatosaurus* can be interpreted as an indication of food chain relationships between the two genera, the former playing the food role of a primary consumer fed upon by the latter, which played the role of a secondary consumer in the freshwater communities in which they lived. The pattern would, of course, be more complicated, since fishes and labyrinthodonts probably provided an additional food supply for the maintenance of the *Chasmatosaurus* populations, and since *Lystrosaurus* could have provided food for other pond predators, such as the big rhinesuchids that have been recorded in the *Lystrosaurus* Zone (see Watson, 1962). But the widespread occurrence of the *Lystrosaurus-Chasmatosaurus* association and the relative abundance of the former in the deposits are to be considered as good indications that the relationships of both these genera represented the dominant channel of energy flow in the food web of the communities to which they belonged.

Garjainia has been found in the deposits of the Russian Zone V, which is considered equivalent to the *Lystrosaurus* Zone. It is, in our belief, the first known erythrosuchid, and its position in the fossil record agrees with its possession of several intermediate features between proterosuchids and erythrosuchids (Charig and Reig, *in press*). The dentition is more carnivorous, and the skull shows modifications for a more efficient biting mechanism. The postcranial skeleton is unfortunately very little known. The skull characteristics of this genus are better developed in later erythrosuchids.

The way of life of more advanced erythrosuchids may be inferred from the skeletal morphology of the upper Lower Triassic genera (*Erythrosuchus, Shansisuchus, Vjushkovia*). Von Huene (1911: 20) pointed out that *Erythrosuchus* should be considered a mainly aquatic predator ("ein sich viel im Wasser aufhaltendes Raubtier"), maintaining that its enormous head can hardly be supposed to belong to an entirely terrestrial animal and that the same conclusion is supported by the structure of the remainder of the body ("Der plump Körper, der kräftige, aber relativ nicht lange Schwanz und namentlich der des grossen Schädels wegen aussergewöhnlich kurze Hals unterstützen die Annahme, das *Erythrosuchus* sich meist im Wasser aufhielt [Flüsse oder Tümpel]."). Tatarinov (1961: 131), on his part, although accepting that "the general proportions of its body, with a relatively huge head and short legs" indicate that erythrosuchids were tied to the water, seems inclined to believe that

they were relatively more terrestrial than the proterosuchids, and stressed the carnivorous specializations of these animals, saying: "The main difference of the erythrosuchids with respect to the proterosuchids is related to the passage to an active carnivorous way of life" (Tatarinov, 1961: 130). We doubt that bulky and clumsy animals like *Erythrosuchus* or *Shansisuchus* should be considered very active animals, a point that has been emphasized by Young (1964: 146). It is more likely that they were inhabitants of swamp marshes, able to prey upon big, slow herbivorous vertebrates, inhabiting the same environments, which could be caught by a relatively slow and heavily built predator. In this connection, we may explore the question of what animals were the prey of the erythrosuchids.

Although evidence of certain association is not abundant, it is meaningful that the erythrosuchids can be considered animals that belonged to the same communities inhabited by the big, upper Lower Triassic dicynodonts of the families Kannemeyeriidae and Shansiodontidae (for a modern survey of these dicynodonts, see Cox, 1965). The most reliable association data are probably those coming from the deposits of the Ermaying Formation in China (Young, 1964; Sun, 1963). In several localities of this formation, bones of *Shansisuchus* and of *Erythrosuchus* were found, although not in actual association. Pearson (1924: 851) maintains that *Kannemeyeria* was a terrestrial animal that probably used its well-developed paws for digging or scraping in order to obtain its food, and she reported that Watson supposed that *Dicynodon* and *Kannemeyeria* lived on dry land. The origin of the giant dicynodonts of the Kannemeyeriidae is not well known but, as Cox (1965) has stated, the dicynodonts are hardly derivable from the aquatic and specialized lystrosaurids of the earlier level of the Lower Triassic. More probably they originated from some member of the vast array of Upper Permian dicynodontids, which are commonly considered herbivorous reptiles well adapted to living in terrestrial environments (see Watson, 1960: 201). The Middle Triassic representatives of the same group (kannemeyeriids and stahleckeriids) provide good evidence of association with terrestrial reptiles.

It can be argued that if the giant kannemeyeriids are derivable from the terrestrial herbivorous dicynodonts of the Upper Permian, the Lower Triassic Kannemeyeriids and shansiodontids should be also considered as upland dwellers. We believe, however, that this conclusion is not necessarily valid, and that the heavily-built and big-headed kannemeyeriids may be better thought of as inhabitants of shallow waters.

Moreover, there is no reason why, if the Upper Permian terrestrial dicynodontids should have been able to evolve into the fully aquatic lystrosaurids, they could not also have been the ancestors of semi-aquatic marsh dwellers. Therefore, Pearson's interpretation of the habits of *Kannemeyeria* cannot be taken as conclusive.

If this reasoning is correct, proterosuchian evolution during Lower Triassic times can be interpreted as a shift from the aquatic and swimming predaceous way of life as represented by the proterosuchids, towards a shallow-water predaceous way of life, the shallow-water predators being adapted for slow walking in swamps. In the first case the main prey was the aquatic lystrosaurids, in the second case, the giant marsh-dwelling herbivorous kannemeyeriids.

In support of this conclusion, it is meaningful that the high point of the proterosuchids occurs in the *Lystrosaurus* Zone and equivalent levels of the lowermost Triassic, and that the erythrosuchids began to be abundant once *Lystrosaurus* itself became extinct. This seems to indicate that the shift in proterosuchian evolution from an aquatic towards a lowland marsh environment was necessitated by the extinction

of the main source of food of the proterosuchid populations: the aquatic lystrosaurids. Once these became extinct, the originally aquatic proterosuchians were forced to look for their prey in the large herbivorous dicynodonts inhabiting the lowland marsh regions. This triggered the development of improvements for a walking locomotion and for large animal predation, both of which are characteristics of erythrosuchids. The sprawled condition of the legs is less efficient than the upright stance in a walking animal, but the latter is not completely necessary for slow animals hunting in shallow water environments for sluggish herbivores. This may explain how the erythrosuchids were successful animals in spite of the fact that they were sprawled and not very active predators and, at the same time, why they developed improvements for a walking locomotion as compared with the proterosuchids. In this sense, the changes in appendicular skeleton shown by the erythrosuchids, which do not reach a full degree of fitness for a terrestrial active locomotion, can be satisfactorily explained as an adaptive level suitable for a marsh dweller, and as a prospective adaptation (or a "preadaptation") for future terrestrial locomotion.

The fossil record also indicates that the proterosuchids did not become completely extinct after the *Lystrosaurus* zone and the extinction of the lystrosaurids, as one species of *Chasmatosaurus* has been reported in beds equivalent in age to the *Cynognathus* Zone (Young, 1964). Seemingly, the proterosuchids remained in their old environment as such, but were reduced in number and variety and played a secondary role in the aquatic communities. These aquatic proterosuchids from the upper part of the Lower Triassic, surviving after the detachment of the erythrosuchids, may well be the source of the other aquatic groups of archosaurs present in the record at later levels in the Triassic period.

The erythrosuchids seem to have become extinct by the end of the Lower Triassic. From the very beginning of the Middle Triassic other large predaceous archosaurs have been found in different parts of the world, representing a more terrestrial type; most of these belong to the family Rauisuchidae of the pseudosuchian thecodonts. At the same time, the evidence seems to indicate that at least some kannemeyeriids shifted towards a more terrestrial life in middle Triassic times, as their remains have been found associated with typical upland reptiles. The extinction of the erythrosuchids, however, and their replacement by more terrestrial thecodonts better adapted for upland and active locomotion could also be explained by a change in habitat of the animals representing the main source of food for carnivorous archosaurs. But in this case, the replacing group is not derivable from the replaced one, as the rauisuchids seem to have evolved from another group of Lower Triassic thecodonts, the pseudosuchians of the family Euparkeriidae. It will be of interest now, to review our knowledge of the proterosuchian descendants.

PROTEROSUCHIAN DESCENDANTS

It is here maintained that the Proterosuchia may be considered the stem archosaurian group, in which most of the subsequent evolution of archosaurs is rooted. The ways in which descent took place remain, however, rather obscure.

The taxa which seem most likely to have been derived directly from the proterosuchians are the Pseudosuchia and the Crocodilia. Saurischians and phytosaurs are also likely to be direct derivatives of the proterosuchians, but the evidence is far from being conclusive. The Ornithischia and the Pterodactyla are better thought of as descendants of the Pseudosuchia, but we are lacking the relevant data to advance any more secure opinions about them.

This theory does not agree with the classical view, which considers the pseudosuchian thecodonts as the ancestral

group of later archosaurs, claiming that a tiny and bipedal pseudosuchian was the prototypical archosaur forebear from which the various dinosaurs, the pterodactyls, the crocodiles, and even the birds could have arisen. According to this view, bipedalism and small size, combined with fully terrestrial habits, are to be considered as primitive archosaur characteristics. We believe this widely-accepted hypothesis to be outdated and in direct contradiction to the evidence gathered in recent years. We shall develop our points of view in a brief analysis of some of the critical details.

Classification and evolutionary significance of the Euparkeriidae

The origin of the Pseudosuchia from the Proterosuchia is strongly supported by the existence of such an intermediate thecodont genus as *Euparkeria,* from the *Cynognathus* beds of the South African Karroo succession. *Euparkeria* has been recently revised by Ewer (1965) in an elegant work that added a great deal of information to our previous knowledge of it. Its evolutionary significance has been also discussed by this author and by Hughes (1963). It is profitable to make an additional analysis of the bearing of *Euparkeria* upon the classification and phylogeny of the thecodonts.

Ewer emphasized the intermediate nature of *Euparkeria.* This genus is remarkable for the fact that it shares proterosuchian and pseudosuchian character-states, which, of course, is the reason for the different familial allocations given to it by various authors. Both Ewer and Hughes are inclined to place *Euparkeria* within the Proterosuchia as a member of the family Erythrosuchidae. Previous authors generally placed *Euparkeria* within the Pseudosuchia (1) as a member of the family Ornithosuchidae (Tatarinov, 1964), (2) in a family of its own, Euparkeriidae (von Huene, 1920; Romer, 1956; von Huene, 1956), or, (3) rather oddly, in the family Sphenosuchidae (von Huene, 1962). Broom (1913), Heilman (1926), and Watson (1957) emphasized its central position among the Pseudosuchia, and thought of *Euparkeria* as a genus typifying the group from which the main lineages of the later archosaurs could have arisen.

Euparkeria shares with the Proterosuchia the following character-states of our list: 1, 2, 8, 9, 10, 12, 14, 15, 22, 23, 24, 26, and 28. This means that it has in common with the proterosuchians thirteen of the twenty-nine items of our analysis, and that it differs in the remaining sixteen. If we should apply a taxonomic criterion based on overall resemblance, *Euparkeria* would have to be placed in a taxon distinct from the Proterosuchia. Our approach is not, however, a phenetic one, and we are more attracted toward an evaluation of the character-states of this genus from an evolutionary point of view.

Eleven of the thirteen character-states shared by *Euparkeria* with the proterosuchians belong to our *AS* class. They are primitive archosaurian (and pre-archosaurian) features that evolved slowly during the first states of the archosaurian evolution. On the other hand, as these character-states are present in all the proterosuchians, they do not afford clues by which to investigate the affinities of *Euparkeria* within the Proterosuchia. More significant is the agreement of this genus with the proterosuchians in two of the three *SS* character-states: the presence of palatal teeth and the presence of intercentra.

Palatal teeth are known to be possessed by the proterosuchids, but not by the erythrosuchids. Intercentra are present in *Euparkeria* through all the length of the presacral vertebrae, just as in *Chasmatosaurus. Erythrosuchus* is the only erythrosuchid having intercentra, and they are present only in the cervical region of the column. These facts could be interpreted as an indication that the erythrosuchids were not the ancestors of the euparkeriids, and that the latter arose somewhere within

the proterosuchids as a separate lineage. However, the erythrosuchids show features in the dentition, the skull, and the appendicular skeleton, that relate them more closely to the euparkeriids than to any of the proterosuchids. If one were to infer relationships by overall resemblance, it would be safe to conclude that the euparkeriids are more closely related to the erythrosuchids than to the proterosuchids. Palatal teeth and intercentra are, in spite of that, a true challenge to erythrosuchid derivation. An additional hint in the same direction is afforded by the presumed way of life of *Euparkeria.* As Ewer pointed out, this genus was a predator upon tiny vertebrates and invertebrates living in upland regions, and, as such, was capable of rapid locomotion in a terrestrial environment. This kind of animal is hardly derivable from such bulky and sluggish marsh dwellers as the contemporary erythrosuchids seem to have been. These contradictions can be overcome if we visualize the origin of the euparkeriids as an event that took place during the transitional phase of the proterosuchid-erythrosuchid descent. At this stage, the transitional forms should have retained some of the primitive proterosuchid character-states, and they should also have acquired some of the morphological and ecological traits of the erythrosuchids. These proterosuchians would have lived in a transitional ecological zone where selective pressures would have rewarded any acquisition for a better adaptation as predators of great size dwelling in lowland marshes, and also any change improving upland fast locomotion, air-wave hearing, biting efficiency, and water economy, all of which are necessary acquisitions for active terrestrial predators. Directional selection would have created, in the first case, the typical erythrosuchids; in the second case, the euparkeriids.

It is meaningful in this connection that the euparkeriids differ from both erythrosuchids and proterosuchids precisely in those characters that can be correlated with functions linked with upland rapid locomotion, air-wave hearing, masticatory efficiency, and, presumably, water economy. *Euparkeria* shows changes to a different state in, among others, items 16, 17, 18, 19, 20, 21, and 25 of our list of proterosuchian character-states. In all those cases, the changed state of the character in *Euparkeria* was evidently linked with improvements for a more efficient terrestrial locomotion: upright stance; hind limbs longer than the fore limbs to a greater degree than in the proterosuchians; femur without intertrochanteric fossa or internal trochanter; humerus with less expanded ends; tarsus with incipient specializations in the ankle joint, thus anticipating developments in the later pseudosuchians; a longer pubis and ischium representing a more advanced type of triradiate pelvis. At the same time, the development of a fully evolved otic notch shown by *Euparkeria,* distinct from proterosuchian character-state 4 and correlated with changes in the state of character-states 5 and 6, is to be interpreted as an improvement for better air-wave hearing, the otic notch being obviously an improved device in this direction, as it gives room for, and enhances the function of, the tympanic membrane.

Concerning the changes in the biting mechanism, Watson (1957) and Ewer (1965) demonstrated how far the shifting forward of the suspensorium, moving the quadrate towards a more vertical position, is a necessary development toward increasing the height of the temporal region and correlatively toward lengthening the fibers of the temporal musculature for a more efficient biting action. This development is fully attained in *Euparkeria,* and in this genus it is correlated with an enlargement of the upper temporal opening, which provides additional area for the insertion of the *pseudotemporalis* muscle, and with the development of a dentition more specialized for a predaceous way of life.

Ewer has convincingly argued against

the interpretation of the antorbital fenestra as an area of insertion of the *pterygoideus D.* muscle maintained by Dollo, Gregory and Adams, and Walker. She stresses the possibility that this fenestra might have housed a large salt gland, as suggested by Broom (1913). It is now well known that not only several marine vertebrates (Schmidt-Nielsen, 1958) but also desert lizards such as *Ctenosaura* and *Sauromalus* (see Templeton, 1964, 1966) have nasal salt glands that play an important role in removing chloride salts from the body, with a small loss of water, thus acting as an extrarenal mechanism for salt excretion and water economy. The known cases of the presence of nasal salt glands of this sort in living vertebrates do not show this gland housed in an antorbital fenestra, but we do not believe that this fact need be a serious challenge to the interpretation of Broom and Ewer. Though admittedly highly speculative, the following reasoning is presented as a possible explanation of the known facts concerning this problem.

As the mammals are urea-secreting animals derived from the pelycosaurs through the therapsids, it can be assumed that the pelycosaurian ancestors of the archosaurs were also ureotelic animals, and that uricotelism developed only later in their archosaurian descendants (the birds are typically uric acid-secreting animals). Uricotelism being related with water economy in animals living in dry conditions, the lack of this metabolic device in the increasingly upland dwelling archosaurs may have been balanced by the development of an extrarenal salt-secreting device. If the antorbital fenestra is actually the site for a salt gland, this may explain the characteristic development of such an opening in all the archosaurs. In this connection, *Euparkeria* clearly shows an improvement beyond the proterosuchian level, as it has a larger antorbital fenestra lodged in a basin-like depression, which indicates a bigger size, and hence, an intensification of the function of the salt gland. This intensification of function of an extrarenal salt-secreting organ can be thought of as an improvement of the adaptation to upland, dry environments, in ureotelic animals coming from a freshwater environment in which economy of water was not necessary. The presence of a small antorbital fenestra in *Proterochampsa* and later crocodiles agrees with this argument; the presence of a large antorbital fenestra in phytosaurs, however, is not consistent with it.

For all these reasons, it seems evident that *Euparkeria* has departed from the proterosuchian level of evolution in significant respects. As most of its innovations are also well developed in the pseudosuchian thecodonts, it is reasonable to think of it as a member of the group representing the early shift of the thecodonts towards the upland life to fulfill the roles of terrestrial carnivorous reptiles, a shift that triggered the radiation of the Middle and Upper Triassic pseudosuchians. In this sense, the new character-states shown by *Euparkeria* in locomotion, biting mechanism, hearing, and water economy are to be interpreted as key innovations opening up new evolutionary possibilities and enhancing the emergence of a new major taxon, which in this case is the suborder Pseudosuchia of the Thecodontia.

In spite of the fact that *Euparkeria* (with *Browniella* as a junior synonym) is the only Lower Triassic slightly-built pseudosuchian known from skeletal remains, the available evidence shows that thecodonts that had already attained the same level of evolution were widespread in upper Lower Triassic and lower Middle Triassic times. This evidence comes mainly from ichnological data, which indicates that quadrupedal, lightly built, and small-sized pseudosuchians flourished by that time in North America (Peabody, 1948). As contended by this and other authors, it is quite probable that the large manus footprints of the chirotheriids of small size were actually made by euparkeriid the-

codonts. At the same time, it is also possible that some dubious skeletal remains of the same general age could in the future be demonstrated as belonging to the same family. *Wangisuchus,* a genus based on fragmentary remains of various individuals, has been referred by Young (1964) to this family. The basis for this assignment is not clear, however.

The known skeletal structure of *Euparkeria* makes it clear that this genus had not attained certain of the specializations that are full-fledged in the Middle and Upper Triassic pseudosuchians that are probably euparkeriid derivatives. This fact supports the splitting off of *Euparkeria* into a family of its own, distinct from the remaining families of the Pseudosuchia. As far as the relationships of the euparkeriids with the other pseudosuchians are concerned, one could say that with respect to the remaining pseudosuchians, the euparkeriids hold the same relationship that the Proterosuchians hold with respect to the whole of the non-proterosuchian archosaurs.

Relationships with the Pseudosuchia

The remaining Middle and Upper Triassic thecodonts are far from affording a clear-cut picture of their evolutionary relationships and classification. It has been said that the Pseudosuchia are a sort of waste-basket, a statement that seems to cast serious doubts about the naturalness of the group. The Pseudosuchia seem to be, however, a natural group, but it is evident that the whole taxon is in need of a thorough revision. Some recent papers by Krebs (1963, 1965), Reig (1961), Sill (1967), Walker (1961, 1964, 1966), and others have already contributed to a great extent to clearing up the status of parts of this taxon.

It is now agreed that the Elachistosuchidae must be ruled out of the Pseudosuchia, as *Elachistosuchus* has been demonstrated by Walker (1966) to belong to the rhynchocephalians. At the same time, Sill (1967, see also below) suggested that the crocodiloid thecodonts usually placed in the superfamily Sphenosuchoidea of the Pseudosuchia, are better considered as belonging to the protosuchian crocodiles. After these deletions, the main subordinate taxa of the Pseudosuchia are the Lower (and Middle?) Triassic Euparkeriidae, the Middle Triassic Rauisuchidae, the Middle and Upper Triassic Stagonolepididae (see below) and the probably related Upper Triassic Stegomosuchidae,[1] the Upper Triassic Ornithosuchidae, and the Upper Triassic Scleromochlidae. It will now be useful here to assess the main conclusions that can be drawn from present knowledge of the pseudosuchians (Fig. 10).

All pseudosuchian families share the following characters: possession of an otic notch; suspensorium shifted forward; V-shaped contour of the posterior border of the lower temporal opening; large antorbital fenestra lying in an extended basin-like depression (with the exception of *Rhadinosuchus* and *Clarenceia,* see later); fairly large nares close to the antorbital fenestra (same exceptions); pterygoids joined at the midline; palatal teeth absent (with the exception of *Euparkeria*); marginal teeth subheterodont and thecodont; intercentra absent (with the exception of *Euparkeria*); advanced quadrupedal or bipedal gait; posterior limbs somewhat longer than the front ones; propodials vertical in position; pes "crocodiloid," with astragalocrural—calcaneum-tarsal ankle joint (incipiently so in *Euparkeria*); calcaneum with a tuberosity; long pubis and ischium; well-developed dermal armor (except in *Scleromochlus,* surely a secondary loss). It seems clear that the above intension of the concept of Pseudosuchia makes this taxon a well-defined one with respect to the Proterosuchia.

The pseudosuchian character-states evolved seemingly as an adaptation to

[1] Walker (1968), however, has recently maintained that the Stegomosuchidae are crocodiles; see Addendum.

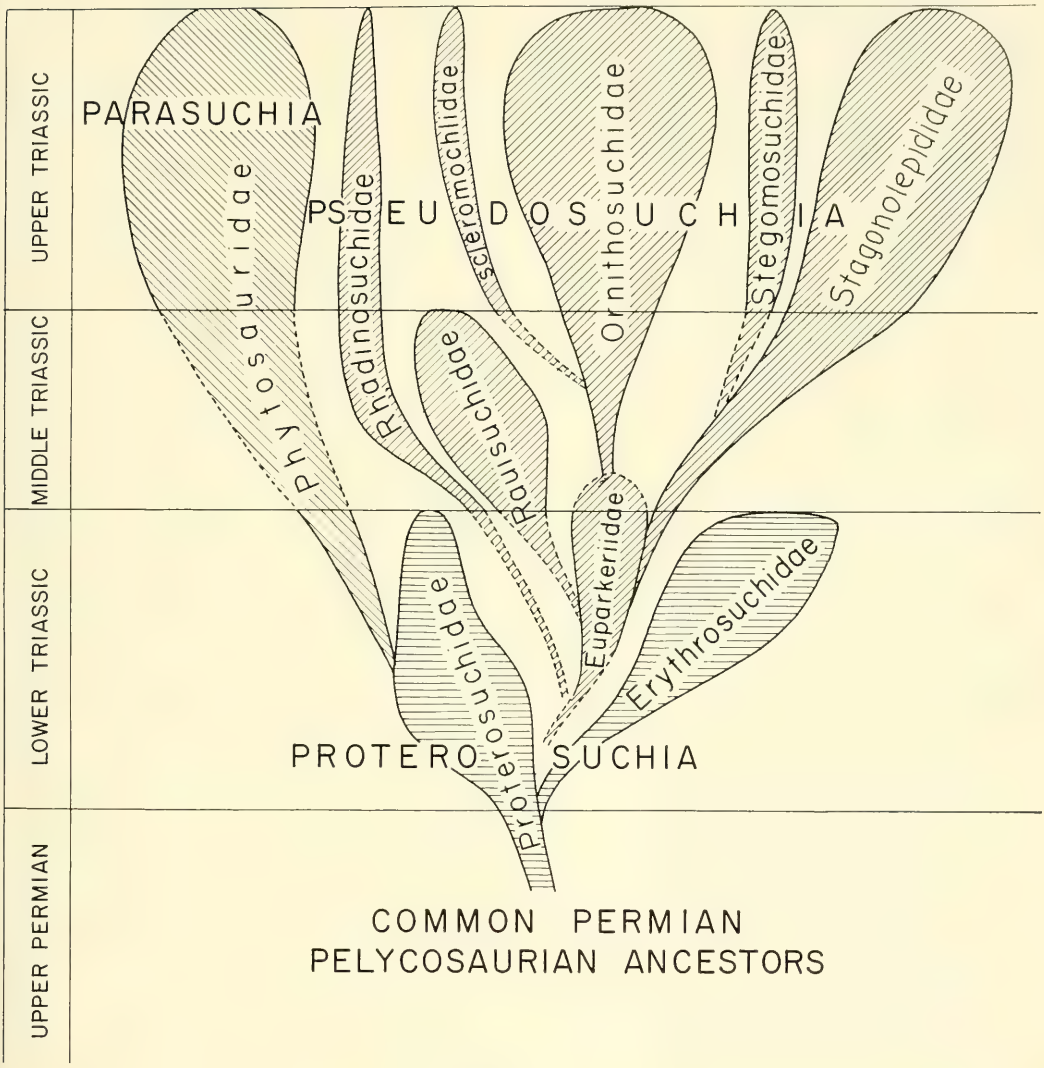

Figure 10. Phylogenetic diagram of the suggested relationships among the various families of the Pseudosuchia and the other thecodonts.

terrestrial life, and for the most part they were already established in the euparkeriids. The rauisuchids probably evolved as a branch divergent from the euparkeriid stock in the early Middle Triassic or uppermost Lower Triassic. Their first well-documented representative is *Ticinosuchus* from the Anisian of Europe (Krebs, 1965). Young (1964) referred to the same family the upper Lower Triassic Chinese genus *Fenhosuchus* because of some similarities in vertebral morphology, shape of the scutes, and other dubious characters. This genus is known from fragmentary bones of various individuals, and its status is far from clear. Nevertheless, the presence of rauisuchids in the Lower Triassic is suggested again by the ichnological evidence, as large-sized quadrupedal chirotheriids of probable rauisuchid relationships have been

found in beds of Scythian age in Germany, North America, and South America (see Peabody, 1948, 1955; Krebs, 1965). Apart from those mentioned above, rauisuchids are known in Middle Triassic (lower Ladinian?) beds of Africa (*Stagonosuchus* of the Manda beds of Tanganyika) and Brazil (*Rauisuchus, Prestosuchus* from the Santa Maria beds of Rio Grande do Sul) and in the upper Middle Triassic (upper Ladinian?) of Argentina (*Saurosuchus* from the Ischigualasto beds of San Juan Province). The rauisuchids seem to have been reptiles well adapted for terrestrial life, and they reached a great size. They were surely huge predators more active and efficient than the erythrosuchids, but they remained quadrupedal like the latter, perhaps because of the attainment of a bulky body and a great weight before the full acquisition of the necessary limb modifications for bipedal stance and locomotion. Advance beyond the euparkeriid level is shown, however, in the full development of a crurotarsal crocodiloid ankle joint, the great elongation of the ventral pelvic bones, the loss of palatal teeth, and the pterygoid union at the midline (as shown in *Saurosuchus*, unpublished personal data), the loss of postparietal and postfrontal bones, and large size. The rauisuchids became extinct at the end of the Middle Triassic, apparently without giving rise to any other group, and perhaps because of the competition of the carnosaurian saurischians. It is also probably meaningful that their spread and diversification from the beginning of the Middle Triassic can be correlated with the extinction of the erythrosuchids at the end of the Lower Triassic.

Another well-defined family of pseudosuchians is the Stagonolepididae.[1] Reig (1961), Walker (1961), and Krebs (1965) have demonstrated that the stagonolepidids are not as closely related to the rauisuchids as is maintained by some authors. Nevertheless, Reig's contention that the two families must be placed in different suborders now appears too exaggerated a view, as it is quite possible that the two families originated in the euparkeriids. The stagonolepidids are, of course, a very clear-cut group, as their specializations in bony armor and in skull and dentition are unique among the thecodonts. That the family was fully established in upper Middle Triassic times is demonstrated by *Aëtosauroides* from the Ischigualasto beds of Argentina (Casamiquela, 1961). They may have separated from the euparkeriid stock in early Middle Triassic times, evolving as an independent lineage that played its own distinct ecological role. *Aëtosaurus* from the German Keuper, *Stagonolepis* from the Elgin Sandstones of Scotland, and *Typothorax, Desmatosuchus, Acompsosaurus,* and *Stegomus* from the Upper Triassic of North America demonstrate that the family was rather widespread in Keuper times.

Though the way of life of the stagonolepidids is still a matter of controversy, it is evident at least that the members of this family were completely terrestrial pseudosuchians and that they are to be regarded as the first archosaurs that were not predators. Walker has supposed that they were mostly herbivorous, while Sawin (1947) maintained that they were scavengers. It is interesting to realize that the stagonolepidids share some general resemblance with the dasypodids, both in the possession of dermal armor and in the general shape of the skull and dentition, a point that would bolster the scavenger hypothesis, but which does not necessarily exclude the assumption of a rather com-

[1] I agree with Walker in including in one family all the genera of thecodonts currently referred to the families "Stagonolepidae," Aëtosauridae, and Desmatosuchidae. The correct familial name for this assemblage is Stagonolepididae Lydekker, July 1887, a name that antedates Aëtosauridae Baur, September 1887. Von Huene's "Stagonolepidae" (1908), so frequently encountered in the literature, is etymologically incorrect.

posite and variable diet, with vegetables and arthropods as usual components.

Stegomosuchus and *Dyoplax*, from the Upper Triassic of North America and Europe, respectively, are rather poorly known genera showing several resemblances to the stagonolepidids in armor development and other features. They may be closely related to the aëtosaurids in origin, but if they are really related to each other, they should be placed in a separate family Stegomosuchidae.

The taxonomic status and the relationships of the remaining pseudosuchians are less clear. Most of the non-rauisuchid and non-stagonolepidid genera are commonly grouped in the family Ornithosuchidae, which is supposed to include small or medium-sized, bipedal predators, of which *Ornithosuchus* would be a typical example. However, this genus has been recently demonstrated by Walker (1964) to include fairly large animals, and the large *Dasygnathus* from the same Elgin Sandstones that yielded the original remains of *Ornithosuchus* is placed by him in its synonymy. Walker also arrives at the odd conclusion that *Ornithosuchus* is neither a pseudosuchian nor any other kind of thecodont, but that it is better placed within the order Saurischia. This latter view is rather difficult to agree with, and the present author has not found in Walker's new data and appraisals sufficient supporting reasons for such an astounding upheaval of the current arrangement.

It is true that *Ornithosuchus* looks like the carnosaurian dinosaurs in several respects, but the instances of resemblance are better ascribed either to the sharing of general archosaurian features or to the fact that *Ornithosuchus* and the carnosaurs attained, in parallel, specializations for bipedal locomotion and a predaceous way of life. On the other hand, Walker did not attempt to demonstrate that this genus is not a pseudosuchian, his argument being directed to support of the view that it is a carnosaur. We think that important reasons are at hand for keeping *Ornithosuchus* in the Pseudosuchia. One of them is the possession of the double line of paramedial scutes, a character-state shared by the euparkeriids, the rauisuchids, and some genera referred to the ornithosuchids, and which is to be considered as an original pseudosuchian feature from which evolved the armor of such heavily armored forms as the stagonolepidids. No certain evidence of dermal armor is known for the Carnosauria; the alleged carnosaurian scutes from the Upper Cretaceous of India are better referred to ornithischian dinosaurs (see Walker, 1964: 117–119). Another important point is that *Ornithosuchus* has, almost surely, a typical pseudosuchian ankle joint. The carnosaurs, like all the saurischians, have a completely different type of ankle joint, which is hardly derivable from such a specialized structure as the pseudosuchian-crocodiloid tarsus (see below). In other respects, *Ornithosuchus* agrees perfectly with the pseudosuchian character-states. It seems rather bizarre to claim that it is a carnosaur when it is not really separable from the thecodonts. Walker admits that "it might ultimately prove necessary to retain *Ornithosuchus* in the Pseudosuchia" (1964: 110), a statement that does not seem to fit very well with his previous affirmation that only the coelurosaurs and the carnosaurs "need be seriously considered in a discussion of the affinities of *Ornithosuchus*" (1964: 105).

Walker also maintains that *Ornithosuchus* lies morphologically close to the boundary between the pseudosuchians and the carnosaurs, and that phylogenetic relationships are more clearly expressed by placing it with the carnivorous dinosaurs. In fact, this seems not to be the case, as typical carnosaurian and other saurischian dinosaurs have been found in beds definitely earlier than the Elgin Triassic (see Reig, 1963a; Charig, Attridge and Crompton, 1965; Ellenberger and Ginsburg, 1966). These finds clearly prove that by the Middle Triassic several lineages of

saurischians were already differentiated, and this suggests that the origin of the group is to be sought as early as the Lower Triassic. The Upper Triassic *Ornithosuchus* cannot be considered as intermediate for temporal reasons, and there are no cogent grounds for placing it anywhere but in the Pseudosuchia. It is more reasonable to believe that within that suborder of thecodonts, one family attained bipedalism and other carnivorous specializations, paralleling some lineages of contemporary dinosaurs with which it entered in competition. If we retain the family Ornithosuchidae and include in it not only the large-sized *Ornithosuchus*, but also the tiny genera *Saltoposuchus* and *Hesperosuchus*, we may agree that the ornithosuchids paralleled both the coelurosaurs and the carnosaurs in general appearance and ecological roles.

The curious *Scleromochlus* may be considered as an arboreal derivative of the Ornithosuchidae, distinct enough to warrant familial separation. There remain, however, other pseudosuchian genera that are less clear as to family allocation. *Erpetosuchus*, from the Upper Triassic of the Elgin Sandstones, has been commonly classified with the ornithosuchids, but other opinions have resulted in the erection of a family of its own for this genus. Walker (1961) places *Erpetosuchus*, *Dyoplax*, and probably *Stegomosuchus* in the family Erpetosuchidae, an arrangement that seems unnatural to the present author. The place of this genus is better considered as unsettled until a modern revision is undertaken.

As far as *Cerritosaurus* (Price, 1946) from the Santa Maria Middle Triassic of Brazil is concerned, it is almost surely, as suggested by Hoffstetter (1955), a junior synonym of *Rhadinosuchus* von Huene. This genus is very peculiar in the small size of the antorbital fenestra, the size and the position of the external nares, the obliteration of the postemporal fenestra, and the straight posterior border of the lower temporal opening. These features make this genus hardly derivable from the euparkeriids, and some of them are actually proterosuchian, non-pseudosuchian character-states. Nevertheless, it has acquired pseudosuchian status in such characters as the absence of postfrontal and postparietal bones, the presence of an otic notch, and the thecodont and subheterodont dentition. If *Rhadinosuchus* is actually a pseudosuchian, it could represent a family of its own, Rhadinosuchidae, as proposed by Hoffstetter (1955) and accepted by Kuhn (1961). This family might have originated independently within the proterosuchians, reaching the pseudosuchian level in its own way. Another poorly known genus from the Upper Triassic of South Africa, *Clarenceia* (see Brink, 1959), agrees with *Rhadinosuchus* in the structure of the antorbital fenestra and the form of the maxilla, and might belong to the same family (Romer, 1966b, makes this genus a dubious member of the Ornithosuchidae, a position that seems to lack relevant foundations). If our interpretation of *Rhadinosuchus* is right, the implication is that either we accept the Pseudosuchia as a polyphyletic assemblage, or we must allow for the inconvenience of erecting a new suborder to accommodate *Rhadinosuchus* and allies. Our knowledge of these forms is, however, too imperfect to support any formal proposal of changes in the system of the Thecodontia.

The origin of the crocodilia

The crocodiles have been classically considered as descendants of the Pseudosuchia. Within the latter, the Sphenosuchidae from the Upper Triassic of South Africa were considered to be the ancestral group. Primitive crocodilian archosaurs such as *Notochampsa* and *Pedeticosaurus* (from the Cave Sandstone beds of the Stormberg Series of South Africa), *Erythrochampsa* (from the underlying Red Beds, which also yielded *Sphenosuchus*), and *Protosuchus* (from the later Triassic or

earliest Jurassic of Arizona), commonly grouped in the crocodilian suborder Protosuchia, have been regarded as transitional between the ancestral sphenosuchids and the later typical crocodiles (Mesosuchia, Sebecosuchia, Eusuchia). According to this conception, the assumption is made that the crocodiles evolved from primitively bipedal pseudosuchians, and that they returned to a quadrupedal gait as an adaptation to the amphibious way of life (for broader information on these ideas on crocodilian origins, see Haughton, 1924; von Huene, 1925; Colbert and Mook, 1951; Kälin, 1955).

Recently, Sill (1967) has made a thorough reappraisal of the question, on the basis of the bearing of *Proterochampsa* upon crocodilian origins. *Proterochampsa* (Reig, 1959) (Fig. 11) is an obvious crocodile from the late Middle Triassic Ischigualasto beds of Argentina, showing a remarkable combination of primitive, transitional, and advanced character-states. It is the earliest crocodile so far known, and it is definitely earlier than the sphenosuchids reported to be the pseudosuchian ancestors of the crocodiles.

The crocodilian nature of *Proterochampsa* is evident from the morphology of the dorsal surface of the skull, the presence of a rudimentary secondary palate built up by the premaxilla and the maxilla, the sculptured bones of the roof of the skull, and the structure of the vertebral apophyses. Besides this, it is noteworthy that the anterior foot shows the typical carpal specializations of modern crocodiles: elongated radiale and ulnare carpal bones. This is demonstrated by a nearly complete anterior leg found in association with the remains of a coelurosaurian dinosaur in the Ischigualasto beds (Reig, 1963a).[1] The femur and the humerus, known to the author through undescribed specimens associated with skull remains, are also typically crocodiloid. Unfortunately, bones of the girdles have not been found so far. As pointed out by Sill (1967), it is meaningful that *Proterochampsa* is in several respects more crocodilian than the later genus *Protosuchus*.[2]

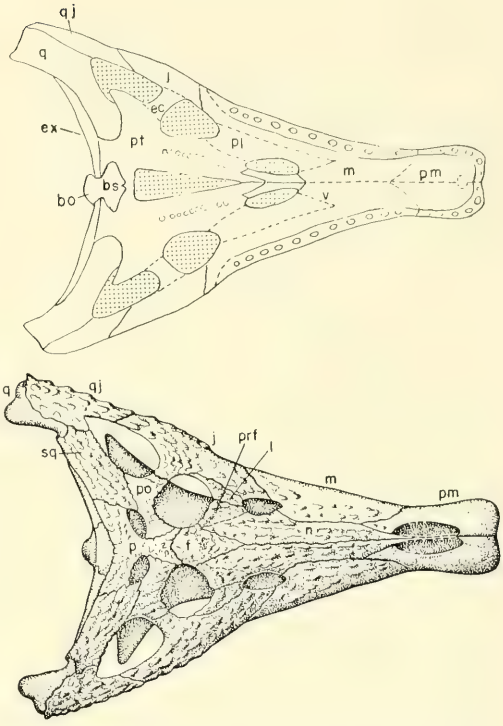

Figure 11. Ventral and dorsal views of the skull of *Proterochampsa barrionuevoi* Reig. (After Sill.)

The implication of the discovery of *Proterochampsa* is that the sphenosuchids can no longer be considered as the thecodont ancestors of the crocodilians, nor can *Protosuchus* and its allies be thought of as a transitional group between the pseudosuchians and the later full-fledged crocodiles. Sill has made a suborder Archaeosuchia to group together both the Middle Triassic monotypic family Proterochampsidae and the Upper Triassic Notochampsidae (including *Notochampsa* and

[1] See, however, the Addendum.

[2] For another view on the place of *Proterochampsa* and other early crocodiles, see Walker (1968) and the Addendum.

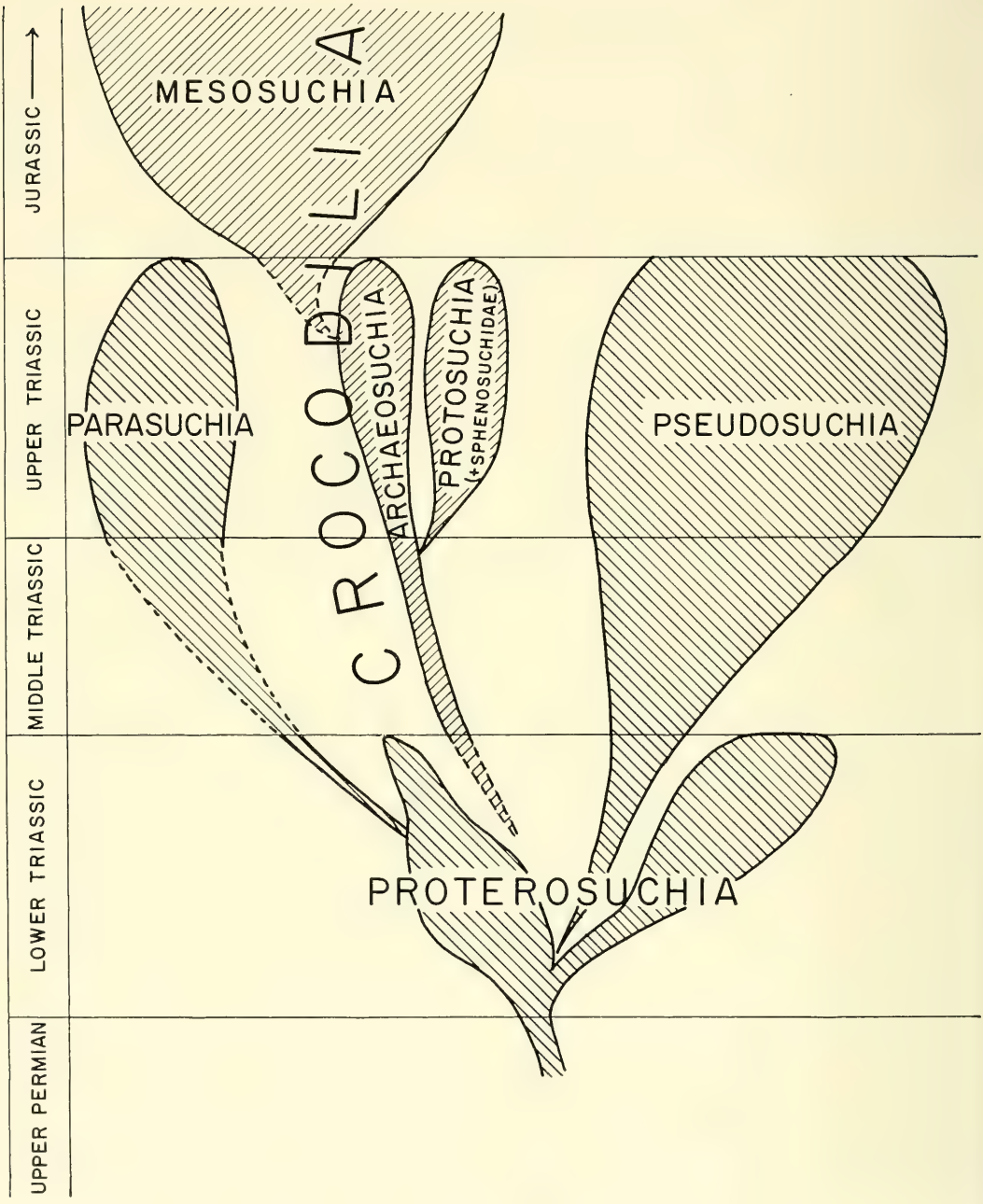

Figure 12. Phylogenetic diagram of the probable origin of crocodiles and the relationships among the various crocodilian and thecodontian suborders.

Erythochampsa). He believes that this suborder is the ancestral group of the Mesozoic and modern crocodiles of the suborders Mesosuchia, Sebecosuchia, and Eusuchia (Fig. 12). *Protosuchus*, on the other hand, would represent a suborder, the Protosuchia of Mook (1934) and later authors, that has departed from the main direction of crocodilian evolution by adaptating to a more terrestrial way of life. As Sill has proposed and Romer (1966b) has accepted, the Sphenosuchidae and such dubious genera as *Pedeticosaurus* and *Platyognathus* are better grouped within the Protosuchia, since they agree with *Protosuchus* in the sharing of an early crocodilian heritage with adaptations for a more terrestrial life. Referring to these animals, Sill uses an expression coined by Kermack: they are "crocodiles trying to be dinosaurs." This meaningful expression describes perfectly the evolutionary trend in these atypical crocodiles for a dinosaur-like (i.e. terrestrial and predaceous) way of life.

Sill advances two alternative hypotheses for crocodilian origins: either they originated from a non-pseudosuchian group of aquatic thecodonts, or they descended from a primitive group of terrestrial thecodonts, possibly early pseudosuchians. As we have already seen, the euparkeriids make perfect early pseudosuchians in their organization. *Proterochampsa* is, however, hardly derivable from euparkeriid ancestors for the following reasons: (1) it has not developed the typical pseudosuchian otic-notch; (2) it has a primitive and small antorbital fenestra; (3) it has not acquired the pseudosuchian V-shaped contour of the posterior border of the lower temporal opening; and (4) it has the suspensorium placed backwards. These are actually proterosuchian character-states, and *Proterochampsa* is also proterosuchian in the possession of palatal teeth and in the shape and proportional size of the temporal openings.

This gives support to the first of Sill's two alternative hypotheses, suggesting that the Archaeosuchia (and through them, all the crocodiles) might have been derived from the aquatic proterosuchians of the Lower Triassic. It should be remembered that after the separation of the erythrosuchids, proterosuchids were represented in beds equivalent to the *Cynognathus* Zone. These late aquatic proterosuchians could have been the ancestors of other lines of aquatic archosaurs.

Nevertheless, one important point remains unexplained if we accept Sill's first alternative. Crocodiles and pseudosuchians (and probably phytosaurs) share the possession of a peculiar type of ankle joint, the so-called "crocodiloid" tarsus, in which the functional joint lies between the astragalus and calcaneum, these being articulated by means of a ball-and-socket type of joint. As we have already seen, this kind of tarsus is not a primitive archosaur characteristic, as both proterosuchids and erythrosuchids show quite another, more primitive, type of ankle. Walker's belief (1964: 110) that the crocodilian ankle-joint "may after all represent a basic archosaurian pattern," is therefore lacking a serious basis. Krebs (1963) has pointed out that the resemblance between pseudosuchians and crocodiles in tarsal structure is so great that it is difficult to think that such a tarsus arose independently in both groups by convergent evolution. It must be realized that the hypothetical common ancestral group for both crocodiles and pseudosuchians, required by tarsal structure, could not be identical with the euparkeriids, as *Euparkeria* has not reached full development of such a type of ankle joint. This means either that the supposed common ancestor should be sought at a post-euparkeriid level of thecodont evolution or that it must be accepted that the character-state under discussion developed independently in pseudosuchians and crocodilians. The first possibility seems to be ruled out, as the characteristics of the archaeosuchians do not permit thinking of

a common ancestry even at the level of the euparkeriids. It would be very useful to have information about the structure of the ankle in *Proterochampsa,* which, unfortunately, is not available thus far.

In our present state of knowledge it seems best to adhere to the hypothesis of the proterosuchian origin of the crocodilians, and to accept the idea of the convergent evolution of the type of ankle found in both crocodiles and pseudosuchians. It must be admitted, however, that the evidence is still too incomplete to permit a fully satisfactory explanation of crocodilian origins, and that a better knowledge of Lower and Middle Triassic thecodonts may make it necessary in the future to introduce changes in the present explanation. At this point, it is interesting to recall the Rhadinosuchidae, a Middle Triassic group of scarcely known thecodonts that seem to have reached the pseudosuchian level from an ancestry distinct from the euparkeriids. It will not be surprising if a better understanding of these forms throws light on questions of the kind raised here.

Saurischian ancestry

The ancestry of the saurischian dinosaurs is also commonly explained by hypotheses that advocate that the pseudosuchian thecodonts were the ancestral group. Until recently, the first unquestionable saurischians were known only from beds of Upper Triassic age; indeed the presence of dinosaurs has been considered conclusive evidence for dating Triassic strata of dubious age as Upper Triassic. Coelurosaurs, carnosaurs, and prosauropods were known from the Upper Triassic, and all three groups were supposed to derive from a single source in the Upper Triassic, namely allegedly tiny, bipedal, carnivorous pseudosuchians similar to the ornithosuchids. According to this conception, the quadrupedalism of the sauropods was secondary and derived from a primitive bipedal condition.

Our intent here is not to essay an exhaustive look at the rather confusing situation of the Triassic saurischians. This task has been partially carried out by Charig, Attridge, and Crompton (1965), Colbert (1964), and Walker (1964), and work by these and other authors will surely contribute to a better understanding of the group. We need, however, to present a very general survey of the present status of knowledge about Triassic saurischians in order to frame the question of saurischian origins as coherently as possible in terms of its factual foundations, and thus to check to what extent the existing stereotyped opinions on saurischian origins are supported by the available evidence.

The Upper Triassic faunas of the world differ sharply from the Middle and Lower Triassic ones in the abundance and variety of their dinosaurs. Romer (1966a) recently made it clear that in spite of semantic discussions on the rather conventional question of the boundary between Middle and Upper Triassic, the faunas currently referred to the Middle Triassic are distinct from those usually referred to the Upper Triassic by the fact that their dominant groups are different. Gomphodonts and rhynchosaurs are dominant in the B assemblages (Middle Triassic); dinosaurs are the dominant group in the C faunas (Upper Triassic). The same synecological criterion has been used in Reig's (1963a) discussion of the age of the Ischigualasto beds, a criterion that seems not to have been sufficiently grasped by Bonaparte (1966) in his recent discussion of the Argentinian vertebrate-bearing Triassic. These Upper Triassic faunas are known in the European Keuper, the Red Beds and Cave Sandstones of South Africa, the Forest Sandstones of Southern Rhodesia, the Dockum and Chinle of North America, and the Lufeng Series of China. The Los Colorados beds and the El Tranquilo Formation of Argentina, the faunas of which are now being studied by Bonaparte and Casamiquela, probably belong to the same group.

Faunas of the B type are known in South America (Santa Maria, Ischigualasto, Chañares), Africa (Manda beds, Molteno beds, Ntaware Formation), and India (Maleri beds). Some faunas, such as those from the Elgin Sandstones (Scotland) and Maphutseng (Basutoland), seem to be transitional between the B and C assemblages.

The saurischians of the late Triassic faunas belong to three different infraorders, which are clearly recognizable at the time of their first appearance in the Lower Triassic, namely the Coelurosauria, the Sauropoda, and the Palaeopoda (I use here Colbert's [1964] new name instead of Prosauropoda, as this last concept is confusing both in intension and in extension). The coelurosaurians are represented in the Upper Triassic by the family Podokesauridae, Hallopidae, and Segisauridae (the second not surely distinct from the first). They were slightly-built upland predators, distinguished from other contemporaneous dinosaurs by the "dolichoiliac" pelvis (Colbert, 1964), advanced bipedal gait, birdlike feet, calcaneum usually with a tuber, long neck, relatively elongated skull. It is now clear that the true Carnosauria of the Jurassic and Cretaceous are an offshoot of the Coelurosauria, with which they share the same type of pelvis, the birdlike feet, and many other features. Both infraorders are therefore grouped in the suborder Theropoda of Marsh, giving to this taxon-concept a narrower extension than that in the current conservative classification.

The Sauropoda are represented from the very beginning of the Upper Triassic by the Melanorosauridae. This family is usually placed within the "Prosauropoda" (= Palaeopoda). Recent work by Ellenberger and Ginsburg (1966) demonstrates that they are quadrupedal and very close to the true sauropods. These authors and Attridge (1963) suggested that the melanorosaurids should be considered true sauropods, a suggestion that seems very reasonable to me. Though disregarding the melanorosaurids as direct ancestors of the sauropods, Charig *et al.* have convincingly demonstrated that "the line of evolution which led from the pseudosuchians towards the sauropods was entirely quadrupedal; thus the sauropods were not, as commonly supposed, quadrupedal reversions from bipedal forebears.

"The various families of prosauropods were offshoots from this main, quadrupedal sauropodomorph line, representing adaptations to different habitats which differed especially in their degree of bipedality; none survived the Trias" (1965: 205). From the new evidence provided by Ellenberger and Ginsburg (1966), one arrives at the conviction that the melanorosaurids should belong to this "main, quadrupedal sauropodomorph line" which, from its very beginning, was part of the evolution of the true sauropods. Melanorosaurids are known from the Middle-Upper Triassic boundary, as represented by the remains referred to *Euskelosaurus* by Ellenberger and Ginsburg (1966), which come from the "Passage beds" of Basutoland (the "Maphutseng dinosaur" of Charig *et al.*, 1965); a hind leg from the same beds described by Crompton and Wapenaar (in press) (reported by Charig *et al.* as the "Blikana dinosaur"); and the "Soebeng trackways," footprints of a big quadrupedal dinosaur, mentioned by the above authors and by Ellenberger and Ginsburg (1966). Besides these early finds, melanorosaurids are relatively abundant in the Red Beds of South Africa. The Melanorosauridae are likely to have been herbivores and swamp-dwellers; the possibility that the family would include carnivorous forms has been suggested by Charig *et al.* (1965), but there are good reasons to doubt this. The evidence supporting such a view is far from conclusive and it is not very likely that these enormous quadrupedal marsh-dwellers could have been sustained by any food other than large amounts of green matter.

The Palaeopoda are represented by the Thecodontosauridae, the Plateosauridae, and the "Triassic carnosaurs." This last group has been demonstrated (Colbert, 1964; Charig *et al.*, 1965; Walker, 1964) not to have any relationships with the true, post-Triassic carnosaurs, and to be closely connected with (or even inseparable from, as maintained by Charig *et al.*, 1965) the first two families. The thecodontosaurids are medium-sized bipedal or semi-bipedal upland herbivores, known from different levels of the Upper Triassic of South Africa, China, Europe, and North America. The plateosaurids are large European and Asiatic (probably also South American) bipedal plant-feeders dwelling in lowlands. The carnivorous palaeopods are here considered as belonging to one distinct family, for which the name Gryponychidae must be used.[1] Though the facts of association of skull and postcranial bones are scarce and dubious, there is enough evidence to show that carnivorous palaeopods were living in the Upper Triassic. The convenience involved in placing these forms in families containing herbivorous dinosaurs is not very great, as one of the current criteria for family separation is distinction in ecological type. It is therefore preferable to separate the gryponychids as a carnivorous offshoot of the palaeopods, though recognizing that they are close to the other two families with which they share the same type of pelvis, tarsus, and limb structure.

All the palaeopods are closely related, and they are also very similar to the melanorosaurids and later sauropods, so that it makes sense to group both palaeopods and sauropods in a suborder Sauropodomorpha as proposed by Charig *et al.* (1965) and accepted by Romer (1966b). Charig *et al.* make a convincing case in claiming that this term, coined by von Huene (1932), is preferable to Pachypodosauria of the same author, a name applied to the unnatural assemblage of sauropods, "prosauropods," and carnosaurs. Within the Sauropodomorpha, the distinction of palaeopods and sauropods as infraorders is meaningful, as it adequately expresses the evolutionary situation. The sauropods seem to have played a secondary role during Triassic times, only evolving to full-fledged diversity and abundance after the close of that period. The palaeopods, most probably derived from a quadrupedal promelanorosaurid or melanorosaurid stock, represent the main radiation of Triassic Sauropodomorpha, and they evolved into both upland and lowland plant-eaters, and upland bipedal carnivores.

What do we know about the probable origin of the three groups of dinosaurs already well established at the very beginning of the Upper Triassic? Not too much, but at least enough to reveal that the history of the sauropodomorphs and coelurosaurs must be traced well back into the Triassic. Saurischian remains are known from the Middle Triassic of Argentina (Reig, 1963a) and Brazil (von Huene, 1942). The Argentinian fossils are rather abundant, and they come from the Ischigualasto beds, a formation that, following Romer (1966a) and Reig (1963a), contains a fossil assemblage that clearly belongs to the B type of faunas representing, perhaps, an upper Ladinian stage (i.e., the latest Middle Triassic). The Brazilian remains occur from the Santa Maria beds, which are generally agreed to be older than the Ischigualasto and roughly equivalent to the Manda beds of Tanganyika.

According to our present knowledge, the Argentinian material represents at least four genera of saurischians, only three of which have been described (Reig, 1963a). One genus is a very small, undescribed coelurosaur. Another coelurosaur is repre-

[1] Both Walker (1964) and Charig *et al.* (1965) have indicated that the name Palaeosauridae cannot be used, as *Palaeosaurus* Riley and Stutchbury is preoccupied by *Palaeosaurus* Geoffroy; Kuhn (1959) created the name *Palaeosauriscus* to replace the first name.

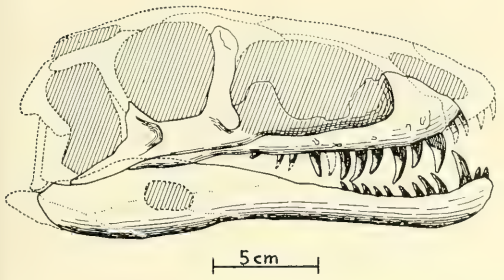

Figure 13. Lateral view of the skull of *Triassolestes romeri* Reig. (From Reig.)

sented by a podokesaurid, *Triassolestes* (Figs. 13, 14), known from skull and postcranial bones of two individuals.[1] The remaining two genera are obviously palaeopods. The best known is *Herrerasaurus*, a fairly large genus with specialized carnivorous dentition and typical palaeopod pelvis and posterior limbs (Figs. 14, 15), but with a peculiarly expanded distal border of the pubis, very like the situation in megalosauroid carnosaurs. As indicated by Walker (1964: 107), this last character-state does not necessarily imply a taxonomic or phylogenetic affinity between *Herrerasaurus* and the Upper Jurassic and Cretaceous true carnosaurs, and the genus must be placed in the Palaeopoda either as a member of the Gryponychidae or as a separate line. The other palaeopodan genus is *Ischisaurus*, known from incomplete remains of different individuals. It is thecodontosaurid-like in size and general appearance, and the small size of the humerus, which hardly exceeds half of the length of the femur, suggests that it was a definitely bipedal form.

A supposed Brazilian dinosaur has been described by von Huene as *Spondylosoma*, on the basis of isolated bones insufficient to allow of even ordinal assignment. Material recovered later, and being at present studied by Colbert, clearly indicates, however, that a saurischian of palaeopodian

[1] See, however, the Addendum.

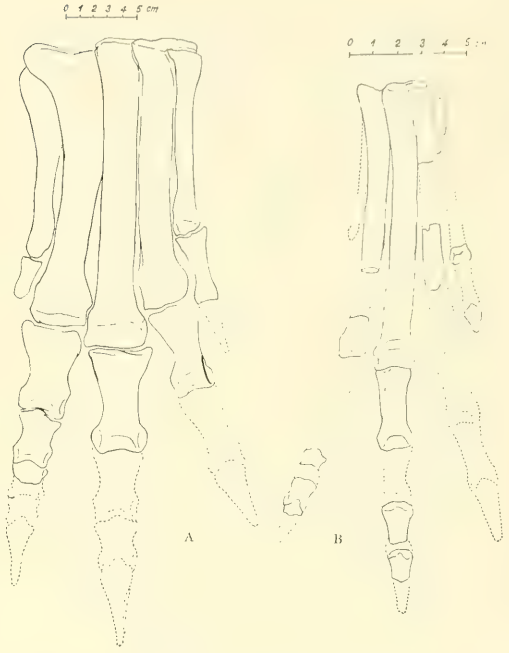

Figure 14. Pes in Middle Triassic saurischians from Ischigualasto, Argentina: A, *Herrerasaurus ischigualastensis* Reig; B, *Triassolestes romeri* Reig. (From Reig.) [See Addendum for systematic position of *Triassolestes*.]

affinities was present in the Santa Maria fauna.

The Sauropodomorpha and the Theropoda were thus well differentiated in the Middle Triassic (Fig. 16). It has been suggested (Charig *et al.*, 1965: 215–216) that these two major divisions of the Saurischia originated independently within the Pseudosuchia of the Middle Triassic.

I believe that there are good reasons to doubt that the sauropodomorphs could have arisen from Middle Triassic pseudosuchians, and I am more inclined to look for their ancestry in the Lower Triassic thecodonts. One important argument for this is the timing, as the origin of the sauropodomorphs must necessarily be placed at least as early as the very beginning of the Middle Triassic. This is the only way to explain that in the upper Middle Triassic they have already split into at least three different families: melanoro-

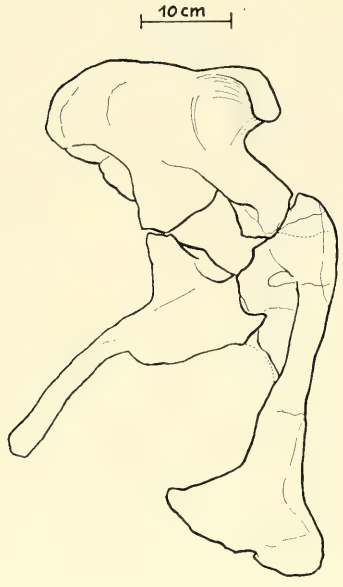

Figure 15. Pelvis of *Herrerasaurus ischigualastensis* Reig. (From Reig.)

saurids, gryponychids, and thecodontosaurids (Fig. 16). The other important argument is ankle morphology. As Krebs (1963) pointed out, the mesotarsal type of ankle joint of the saurischians is hardly derivable from the crocodiloid ankle of the Pseudosuchia. Therefore, the only groups to be considered in sauropodomorph ancestry, as required by ankle morphology, are the euparkeriids and the erythrosuchids, both of which combine the possession of a reduced carpal set with the lack of crocodiloid specializations. In the case of the euparkeriids, Ewer (1965: 431) pointed out that the ankle of *Euparkeria,* in spite of not being specialized as in later pseudosuchians, is advanced a bit towards a pseudo-mesotarsal articulation, which involves eventual elimination of the calcaneum, a situation that could have been ancestral to the "prosauropods" and sauropods. *Euparkeria* is, moreover, slightly built, potentially bipedal, and has dermal armor, all features not to be expected in the ancestor of the originally quadrupedal, morphs. It is more likely that the ancestry of the latter would be within the erythrosuchids, both on ecological and morphological considerations. In fact, it is not difficult to think of the huge, marsh-dwelling, quadrupedal erythrosuchids, with mesotarsal ankle and devoid of any armor, as the ancestors of the quadrupedal, large-sized, unarmored, and marsh-dwelling melanorosaurids (Fig. 16). At the same time, the euparkeriids are likely to be the ancestors of the coelurosaurians, since the evidence indicates that the latter have from the very beginning been upland, rapidly-moving bipedal carnivores, possessing a type of ankle joint which, in spite of being of mesotarsal type, has a calcaneum with a tuber, a condition reminiscent of the crocodiloid pseudosuchian tendencies. At the same time, the fact that at least one coelurosaurian (*Ceratosaurus*) has dermal armor can also be taken as an indication of an early pseudosuchian ancestry.

But, as a matter of fact, it is necessary to realize that we are at the very beginning of an explanation of saurischian origin. The views here advanced on the probable origin of sauropodomorphs from erythosuchid proterosuchians are only to be considered as working hypotheses that, in our belief, match the known facts better than do alternative interpretations. We must admit that these facts are so far not sufficiently complete to warrant a thorough reconstruction of early saurischian history. They are, however, at least complete enough to make it necessary to discard such generally accepted views as that the common origin of all the saurischians lay in bipedal, Upper Triassic pseudosuchians. It is also evident now that the radiation of the saurischians did not start after the extinction of the thecodonts. During Middle and Upper Triassic times, both taxa had their own extensive radiations, apparently developing not only parallel and competitive similar forms, but also forms differing in ecological roles and habitat preferences. The herbivores are by far the less common of the

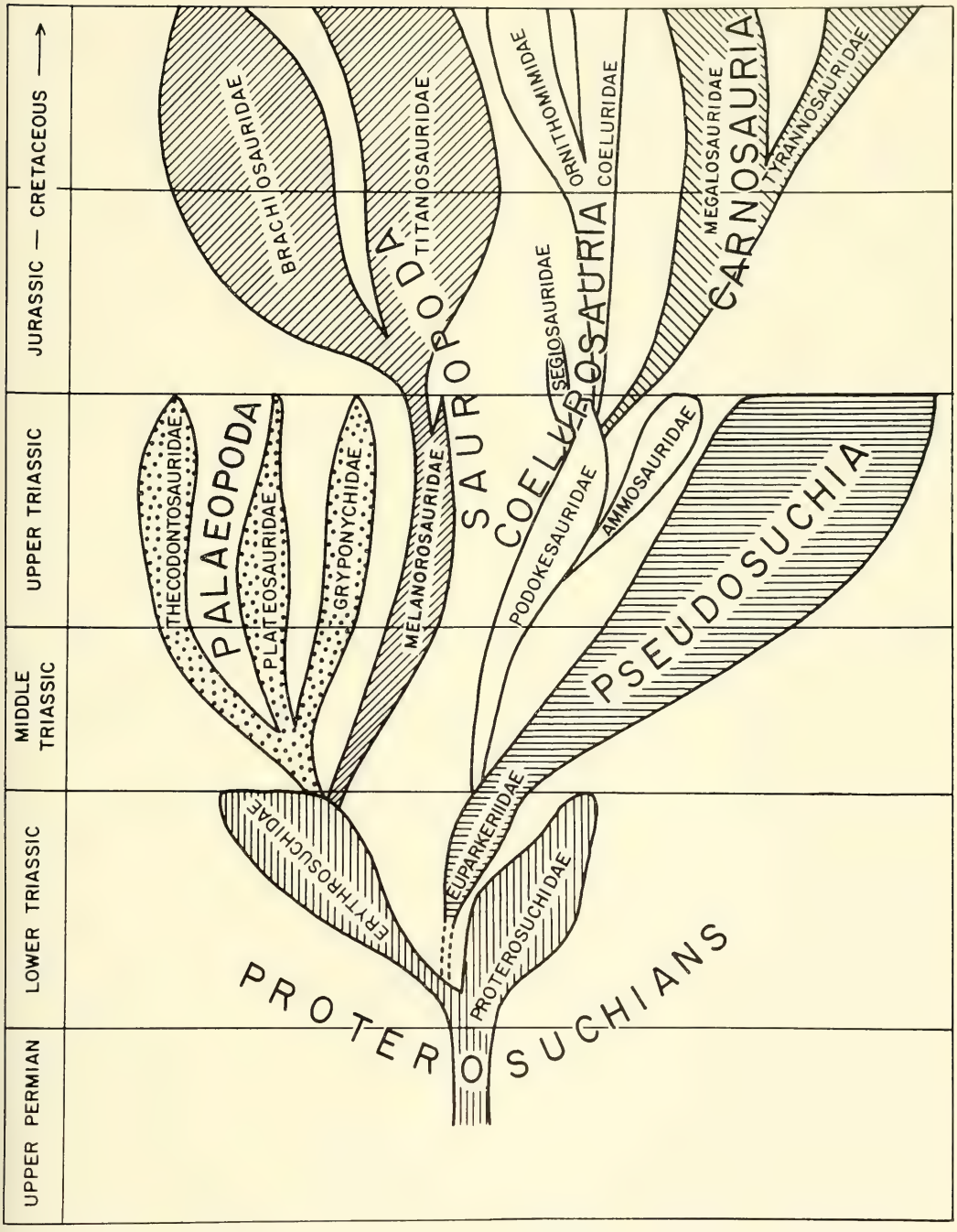

Figure 16. Phylogenetic diagram showing the suggested origins and the relationships of the major saurischian groups.

heavy-built, and unarmored sauropodo-Middle and Upper Triassic pseudosuchians and saurischians, being limited in fact to the stagonolepidids and the melanorosaurids. At these times gomphodonts and kannemeyeroid dicynodonts seem to have been competitors of plant-eating archosaurs.

The case of the phytosaurs and other archosaurian groups

In our present state of knowledge, the relevant evidence for advancing a serious hypothesis of the origin of the Pterodactyla and the Ornithischia is not available. The Pterodactyla, when first encountered in the Lower Jurassic, had already acquired the whole set of specializations for air locomotion. They were probably derived from lightly-built, arboreal pseudosuchians, and the fact that *Scleromochlus* is a genus with these characteristics supports the view that it was connected with the group from which those archosaurs adapted to flying could have arisen. This is as much as can be said at the moment.

As far as the Ornithischia are concerned, this order of dinosaurs, dominant in the Cretaceous, is rather obscure in origin. It has been maintained that the order had its first radiation prior to the Upper Triassic, because of the characteristics of incomplete remains from the Cave Sandstone beds of South Africa, which have been referred to two different genera: *Geranosaurus* and *Heterodontosaurus* (see Crompton and Charig, 1962). The evidence is, however, too fragmentary to support any such conclusion. Walker (1961) suggested that the stagonolepidids might be close to the ancestry of the ornithischians, but in this case also the evidence warrants only highly tentative speculations. The question of ornithischian origins is better considered an open problem until more information becomes available. The lack of relevant data on Triassic ornithischians could also be interpreted as an indication that their origin took place at a rather late stage of archosaurian evolution.[1]

The case of phytosaur origins seems to be a little less obscure, since we are at least able to postulate a probable ancestral group: the proterosuchids. The phytosaurs are a typical Upper Triassic group, and their association with saurischians and metoposaurid labyrinthodonts is the characteristic feature of the C type of Triassic faunas. No certain phytosaur remains are known from the Middle Triassic, but the Lower Triassic of Europe has afforded one skull, which is the basis of the genus *Mesorhinosuchus*, currently referred to this group. Recent work by Gregory (1962) casts some doubts upon the stratigraphic provenance and taxonomic position of this skull, and it must be admitted that the isolation of the specimen with respect to the whole remaining phytosaur record, together with the date and conditions of its discovery, justify a skeptical attitude. The probable presence of a phytosaur in the European Bunter, however, is to be admitted if we assume that the proterosuchians are the most likely ancestors of this group. And this is likely to be the case, since the phytosaurs, aquatic and primitive in postcranial morphology, are hardly derivable from the pseudosuchians, a group that from the outset shows specializations in the appendicular skeleton for a terrestrial way of life that clearly went beyond the level attained by similar advances in the phytosaurs. Admittedly, the phytosaurs share with the pseudosuchians several improvements in general organization, such as the presence of an otic notch, pterygoids joined at the midline, absence of palatal teeth, large antorbital fenestra, absence of intercentra, propodials largely moving in a vertical plane, and well-developed osteoderms. All these features can be interpreted as acquisitions connected with a better

[1] Casamiquela (1967), however, recently described ornithischian remains from the Ischigualasto (upper Middle Triassic) beds. See Addendum.

adaptation both for locomotion on land and for predation that may well have arisen independently in different groups evolving from a proterosuchian condition. Besides these character-states, the phytosaurs show several specializations connected with improvements for aquatic life and aquatic predation: a very long and narrow rostrum formed largely by premaxillaries; external narial openings placed far behind the tip of the snout, close to the midline, between or at a short distance in front of the antorbital fenestra; orbits situated high in the skull; choanae placed posteriorly, and palatines forming lateral shelves below them, etc. The phytosaurs are to be considered specialized proterosuchid derivatives that evolved as amphibious predators, able to live a more efficient aquatic life than their forebears, and at the same time able to move about on the firm land around the water. They were probably very close to the modern crocodiles in biological type.[1]

SUMMARY OF THE MAJOR EVENTS IN EARLY ARCHOSAURIAN EVOLUTION

Improved knowledge of the organization of the first archosaurs, the proterosuchian thecodonts, and a re-examination of present evidence and interpretations of the phylogeny and taxonomy of the main archosaurian groups support the following reconstruction of the early events in the evolution of archosaurs:

1) The archosaurs arose during early Upper Permian times, probably from a branch of aquatic pelycosaurs, the Varanopsidae, which separated from the main line of pelycosaur evolution early in the Lower Permian.

2) During the uppermost Permian and the early Lower Triassic, the first recorded group of archosaurs, the proterosuchid proterosuchians, developed. These were primitive, aquatic predators, living mostly in permanent waters (lakes, ponds, and rivers), as important members of freshwater communities. They survived until the upper part of the Lower Triassic, but dwindled in number and diversity.

3) Some populations of proterosuchids became better adapted to living in shallow waters and improved as predators of large animals. The erythrosuchid proterosuchians arose from such populations, and became dominant in swamps during the upper Lower Triassic.

4) The Pseudosuchia are first represented by the Euparkeriidae of the upper Lower Triassic. These were mostly quadrupedal, rather tiny, upland predators. Their origin is to be sought in the transitional phase of the proterosuchid-erythrosuchid descent.

5) In the uppermost Lower Triassic, the euparkeriids evolved into the rauisuchids. These were the large, quadrupedal, upland predators of the Middle Triassic.

6) The stagonolepidids arose from the euparkeriids in the Middle Triassic, becoming an important group in the Upper Triassic. They were upland dwellers, either scavengers or omnivores.

7) The euparkeriids probably survived through the Middle Triassic, and their last populations gradually were transformed into the ornithosuchids, which became a rather important group in the Upper Triassic as bipedal, medium-sized and large predators.

8) Perhaps on the borderline between Middle and Lower Triassic, the coelurosaurian saurischians evolved from a pseudosuchian, euparkeriid-like source. They were from the beginning bipedal, lightly-built, rapid predators inhabiting the upland environments. They were well established by the upper Middle Triassic, and became diversified and rather abundant in the Upper Triassic.

[1] Walker (1968) has recently advocated that *Proterochampsa* is a phytosaur ancestor (see Addendum).

9) The true carnosaurs evolved in the uppermost Triassic or lowermost Jurassic from a coelurosaurian ancestor.

10) The sauropodomorph saurischians arose as true sauropods in the uppermost Lower Triassic, probably from erythrosuchid proterosuchians, and were four-legged, marsh-dwelling forms from the beginning. These first sauropods were a rather unimportant group in Middle and Upper Triassic times, represented only by the melanorosaurids in the known record.

11) The first important radiation of the sauropodomorphs developed within the framework of the infraorder Palaeopoda. Palaeopod saurischians probably evolved from the first sauropods and radiated in Middle and Upper Triassic times into herbivorous and carnivorous lowland and upland forms. They included partially bipedal and completely bipedal forms.

12) The first crocodiles were the Middle Triassic Archaeosuchia. They probably arose from the last proterosuchid populations of the uppermost Lower Triassic, within the framework of the freshwater communities, but evolved adaptations for a more amphibious way of life. They seem not to have been an important group in the freshwater environments of the Upper Triassic, perhaps because of the competition of the phytosaurs, dominant at this time.

13) During the Upper Triassic, an offshoot of the archaeosuchians became better adapted for terrestrial life and spread as a group of upland predators: the protosuchian crocodiles.

14) The phytosaurs probably evolved from the proterosuchids in the late Lower Triassic as members of the freshwater communities. They were unimportant in the Middle Triassic, perhaps because of the competition of the Archaeosuchia, and became dominant freshwater predators only in the Upper Triassic.

15) By the end of the Triassic, several groups of archosaurs had become extinct: pseudosuchians and protosuchians, and probably archaeosuchians, phytosaurs, and palaeopod saurischians. It was the beginning of the second phase of archosaurian evolution, a phase in which sauropods, carnosaurs, coelurosaurs, mesosuchian crocodiles, pterosaurs, and, later, ornithischians, deployed as full-fledged archosaurian groups.

EVOLUTIONARY AND TAXONOMIC CONCLUSIONS

The foregoing statement of the major events of the early phase of archosaurian evolution and the previous discussion of the evidence supporting such conclusions, are full of implications for the theoretical problems posed on pages 230ff. and 245ff. of this paper.

It will be of interest, now, to examine to what extent the described patterns of origin both of the archosaurs as a major group and of the groups within the archosaurs agree with the current concepts about the processes involved in the emergence of new major taxa. I have already said that a shift into a new adaptive zone, a speeding up of the evolutionary change in the transitional region between the original and the new adaptive zone, and the sudden appearance of key innovations opening new evolutionary possibilities are alleged to occur in the origin of new supraspecific taxa. This process would be responsible for the creation of apparent discontinuities that afford a clear-cut borderline between the original and the descendent groups. We have also seen that Bock (1965) claimed that this alleged pattern is an oversimplification; he emphasized the step-wise character of the process leading to the emergence of a new taxon, a process that he thought of as involving a more complex pattern than any single-phase change from one adaptive zone into another.

Let us examine, first of all, to what extent the shift into a new adaptive zone is

exemplified by archosaur origins and the origin of the subordinate major taxa of archosaurs.

In fact, the origin of the archosaurs as a whole does not seem to be associated with a major shift between two different adaptive zones. The probable archosaur ancestors were water-adapted pelycosaurs, and the first known archosaurs were water-dwelling animals. Both ancestors and descendants seem to have been predaceous animals. Although it must be admitted that a considerable gap exists between the proposed ancestral group and the derived one, the process of the emergence of the archosaurs is likely to have been one of gradual improvement toward a more efficient life in the same general adaptive zone.

As far as the origins of the various archosaurian subordinate taxa are concerned, the pattern seems to have been a mixed one. There is an actual shift from lowland, marsh habitats toward upland environments in the passage from the proterosuchians to the pseudosuchians, but the passage from the proterosuchians to the crocodilians, phytosaurs, and sauropods does not seem to have involved any major departure from the general environments inhabited by the ancestral forms. The same is the case if the coelurosaurians were derived from the euparkeriid-like pseudosuchians. But a shift did occur from the archaeosuchians to the protosuchians. These various cases indicate that a major shift between two distinct general adaptive zones is not necessarily connected with the emergence of a major taxon, though it may occur in certain cases.

If we take a large scale approach, we could, however, agree that there is a major shift in general adaptive zone between the time of the appearance of the archosaurs and the time of their achievement of dominance at the beginning of the Jurassic. The first archosaurs were strictly water-tied animals, swimming and feeding in lakes, ponds, and rivers; the post-Triassic ones were enormous swamp-dwellers and upland forms. The intermediate zone is, however, a long-lasting one, in which various minor radiations took place, and in which there is no reason to postulate any special acceleration of the evolutionary changes.

The hypothesis of an evolutionary speeding up in an alleged transitional zone is also not supported by the known cases of an actual shift. As already stated, the origin of the Pseudosuchia can be considered as one of the cases in which an actual switch seems to have occurred. Nevertheless, we can see here that the process was a gradual and long-term one, and that even the first definite pseudosuchians, the euparkeriids, were transitional in several respects.

Key innovations have arisen, as we have seen, several times in the early evolution of archosaurs. Character-states such as the development of an antorbital fenestra, the acquisition of an otic notch, the shifting forward of the mandibular articulation, the upright stance of the propodials, the pseudosuchian-crocodiloid ankle joint, to mention only some examples, can be safely regarded as being connected with improvements in general adaptability, thereby opening new evolutionary possibilities. It is interesting to realize, however, that features such as the above probably arose independently in different groups, and even that some of them, like the antorbital fenestra, had already evolved at a pre-archosaurian level of evolution.

The general pattern of the emergence of major taxa, as exemplified by the case of the archosaurs, seems to be a pattern of gradual and long-lasting change. At least seven different processes are involved: (1) steady development of the typical characters of the emerging taxon; (2) exploratory radiations into new adaptive zones; (3) competition between lineages that achieve a similar ecological role from different ancestries; (4) steady acquisition of key characters opening new evolutionary possibilities in different lineages;

(5) improvement within the framework of a generally similar adaptive zone; (6) gradual shift into new adaptive zones; and (7) gradual replacement of successive groups until eventually a new, major taxon becomes established. No factors different from those involved at the species or infraspecies level need be involved. Although it may be convenient, for the sake of the description of the evolutionary events, to distinguish the different processes of evolution [as did Huxley (1958) and other authors], it must be stressed that the final agencies of evolutionary change are really the same for any of the processes distinguished in the description of large-scale evolutionary phenomena.

Thus, the emergence of a new taxon can be considered a phenomenon plainly involving only evolution governed by selection and by the known processes of change in gene frequency within populations; the regular processes of evolution at the species level therefore, are also those responsible for the gradual, progressive establishment of major taxonomic groups. On the other hand, the latter are to be considered not as artifacts of classification but as natural units, for they include subordinate entities connected by relationships of origin and descent. But they are not bounded by discontinuities, these being only imposed by the incompleteness of the record. The fact is that the better the evidence connected with the origins of a major group is known, the less apparent are the alleged discontinuities between the ancestral and the descendent groups.

The concepts having natural taxa as referents are hence necessarily polythetic concepts, and a fringe of vaguenesss seems to be unavoidable in the statement of the intension of taxonomic concepts at the supraspecific level. It also seems necessary to agree that vagueness can occur in the statement of the extension of these concepts, as intermediate forms can always be placed in either of the groups they connect.

RESUMEN

Nuevos conocimientos sobre la organización de los tecodontes proterosuquios, que son los más antiguos y los más primitivos reptiles conocidos de la subclase Archosauria, conjuntamente con un estudio crítico de los datos y las interpretaciones actuales sobre la filogenia y la clasificación de los principales grupos de reptiles arcosaurios, dan fundamento a la siguiente reconstrucción de los acontecimientos que tuvieron lugar durante el comienzo de la evolución de los arcosaurios:

1) Los arcosaurios surgieron durante el comienzo del Pérmico superior a partir, probablemente, de una rama de pelicosaurios acuáticos, los Varanopsidae, que se separaron de la línea principal de la evolución de los pelicosaurios en el Pérmico inferior.

2) Durante el Pérmico más superior y el comienzo del Triásico inferior se desarrolló el primer grupo conocido de reptiles arcosaurios, los tecodontes proterosuquios de la familia Proterosuchidae. Los proterosúquidos fueron predadores acuáticos primitivos que vivían en aguas dulces permanentes (lagos, pantanos y ríos) constituyendo una parte importante de las comunidades dulceacuícolas de la época. Sobrevivieron hasta la parte superior del Triásico inferior, aunque en menor número y más reducidos en diversidad.

3) Algunas poblaciones de proterosúquidos se hicieron mejor adaptados para vivir in aguas someras y se perfeccionaron como predadores de grandes herbívoros semiacuáticos. Los proterosuquios de la familia Erythrosuchidae surgieron de dichas poblaciones, tornándose dominantes en los pantanos de la parte superior del Triásico inferior.

4) Los primeros representantes del suborden Pseudosuchia de tecodontes fueron los euparkéridos de la parte superior del Triásico inferior. Eran predadores terrestres de tamaño pequeño y de locomoción

cuadrúpeda. Su origen debe buscarse en la fase transicional de la transformación de los proterosúquidos en eritrosúquidos.

5) A finales del Triásico inferior, los euparkéridos dieron lugar a los rauisúquidos. Estos fueron predadores terrestres de gran tamaño y de andares cuadrúpedos que prosperaron principalmente en el Triásico medio, donde están representados por géneros como *Prestosuchus*, *Saurosuchus* y *Stagonosuchus*.

6) Los Stagonolepídidos (familia que incluye a aetosáuridos y stagonolépidos) surgieron probablemente de los euparkéridos en el Triásico medio, tornándose un grupo importante de las faunas terrestres del Triásico superior. Fueron reptiles terrestres acorazados, de hábitos alimentarios omnívoros, o carroñeros.

7) Es probable que los euparkéridos sobrevivieron durante el Triásico medio, época en la que se fueron transformando gradualmente en los ornitosúquidos. Estos constituyen un grupo de predadores bípedos de tamaño mediano y grande de importancia en las comunidades terrestres del Triásico superior.

8) Es posible que los dinosaurios saurísquios del grupo de los celurosaurios hayan surgido de una cepa pseudosuquia afín a los euparkéridos en la transición entre el Triásico inferior y el Triásico medio. Los celurosaurios fueron desde su origen predadores terrestres bípedos y esbeltos. Estaban ya bien representados en la parte final del Triásico medio, pero se hicieron más abundantes y diversificados en el Triásico superior, donde competían con los ornitosúquidos.

9) Los verdaderos dinosaurios carnosaurios evolucionaron en el Triásico más superior o en el Jurásico más inferior, a partir de un ancestro celurosaurio.

10) Los dinosaurios saurísquios del grupo de los Sauropodomorpha, surgieron como verdaderos saurópodos a finales del Triásico inferior, probablemente a partir de los proterosuquios de la familia Erythrosuchidae. Desde el comienzo fueron animales cuadrúpedos habitantes de los pantanos. Estos primeros saurópodos constituyen un grupo relativamente poco importante en el Triásico medio y en el Triásico superior, donde están representados solamente por los melanorosáuridos.

11) La primera radiación importante de los sauropodomorfos se desarrolló en el marco del infraorden Palaeopoda. Los saurisquios paleópodos surgieron probablemente de los primeros saurópodos y radiaron en el Triásico medio y superior en varias formas herbívoras y carnívoras que vivían tanto en los pantanos como en las tierras altas, entre los que se encontraban animales parcialmente bípedos y otros totalmente bípedos.

12) Los primeros cocodrilos fueron los Archaeosuchia del Triásico medio. Es probable que los arqueosuquios surgieran de las últimas poblaciones de proterosúquidos en la parte más superior del Triásico inferior, en el contexto de la comunidad dulceacuícola, pero desarrollando adaptaciones para una vida más anfibia. No parecen haber sido un grupo importante en los ambientes de agua dulce del Triásico superior, quizás por la competencia de los fitosaurios.

13) Durante el Triásico superior, una rama de los arqueosuquios se tornó mejor adaptada para la vida terrestre y se desarrolló como un grupo de predadores no acuáticos convergente con los pseudosuquios y los celurosaurios: los cocodrilos protosuquios.

14) Los fitosaurios probablemente se originaron en los proterosúquidos a finales del Triásico inferior, en el seno de las comunidades dulceacuícolas. Fueron poco importantes en el Triásico medio, posiblemente por la competencia con los arqueosuquios, pero se hicieron predadores dulceacuícolas dominantes durante el Triásico superior.

15) A finales del Triásico, se extinguieron varios grupos de arcosaurios: pseudosuquios, protosuquios, probablemente también los arqueosuquios, los fitosaurios y los saurisquios paleópodos. Estas extinciones marcan el comienzo de la segunda fase de la evolución de los arcosaurios, caracterizada por la expansión de los saurópodos, los carnosaurios, los cocodrilos mesosuquios, los pterosaurios y los ornitisquios.

Los enunciados anteriores sobre los acontecimientos probablemente suscitados en la fase temprana de la evolución de los arcosaurios tienen variadas implicaciones de interés en la cuestión de la clasificación y el origen de los grupos taxonómicos de rango superior.

El problema del origen de los arcosaurios y de los grupos subordinados de arcosaurios se relaciona con la cuestión ampliamente debatida del origen de los taxa de rango superior. La tesis más difundida para explicar el origen de los taxa de rango superior sostiene que en el proceso de evolución de tales taxa, se produce la invasión de una nueva zona adaptativa, la aceleración del ritmo evolutivo en la zona transicional entre la zona adaptativa original y la nuevamente conquistada, y el surgimiento súbito de innovaciones evolutivas que abren nuevas posibilidades de expansión en la nueva zona. A través de estos procesos, se originaría una clara discontinuidad entre el taxón original y el taxón descendiente, que haría relativamente fácil la distinción entre los mismos. Bock (1965) sostuvo que esa tesis implica una simplificación excesiva de la marcha real de los acontecimientos, y destacó el caracter gradual del proceso de la emergencia de un nuevo taxón, proceso que involucraría fenómenos más complejos que un cambio producido meramente al pasar de una zona adaptativa a otra.

La descripción que hemos hecho en lo que antecede de los principales acontecimientos vinculados con el origen y la primera diferenciación de los arcosaurios, confirma las objeciones señaladas por Bock. El origen de los arcosaurios como tales no parece estar asociado con un cambio adaptativo importante. Tanto los antecesores de los arcosaurios como los primeros arcosaurios (los proterosúquidos) eran animales acuáticos y carnívoros. Es muy probable que el origen de los proterosúquidos sólo haya involucrado un perfeccionamiento gradual hacia una vida más eficiente en la misma zona adaptativa general. El analisis del origen de los grupos subordinados de arcosaurios, indica que tampoco se puede postular un cambio brusco hacia distintas zonas adaptativas como fenómeno inseparable del surgimiento de nuevos grupos. Sin embargo, si observamos el proceso en su perspectiva general, podemos coincidir en la existencia de un cambio en la explotación de distintas zonas adaptativas desde la época de la primera aparición de los arcosaurios hasta la época de la culminación de su dominancia al comienzo del Jurásico. Los primeros arcosaurios eran creaturas estrictamente acuáticas y carnívoras, mientras que las formas jurásicas eran enormes herbívoros terrestres o anfibios y diversos tipos de carnívoros terrestres. La transición entre estos dos extremos, sin embargo, ocupó la mayor parte del Triásico, y durante ese período tuvieron lugar diversas radiaciones exploratorias en el marco de la competencia por la explotación de distintos recursos alimentarios. No queda lugar, entonces, para suponer un proceso en una solo fase ni una aceleración especial de los ritmos evolutivos.

El proceso general de la emergencia de un taxón de rango superior, como surge del ejemplo de los arcosaurios, parece más acorde con la idea de un proceso de cambio gradual y de larga duración, que involucra sencillamente el juego de las fuerzas evolutivas conocidas para la evolución al nivel de la especie: cambios en la frecuencia génica en las poblaciones y selección natural.

BIBLIOGRAPHY

ATTRIDGE, J. 1963. The Upper Triassic Karoo deposits and fauna of Southern Rhodesia. South Afr. J. Sci., **59**(5): 242–247.

BAIRD, D., AND R. L. CARROLL. 1967. *Romeriscus*, the oldest known reptile. Science, **157**: 56–59.

BAUR, G. 1887. On the phylogenetic arrangement of the Sauropsida. J. Morph., **1**(1): 93–104.

BECKNER, M. 1959. The Biological Way of Thought. New York: Columbia University Press, 200 pp.

BEER, G. R. DE. 1954. *Archaeopteryx* and evolution. Adv. Sci., **11**: 160–170.

BOCK, W. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. Syst. Zool., **14**(4): 272–287.

BONAPARTE, J. F. 1966. Chronological survey of tetrapod-bearing Triassic of Argentina. Breviora, Mus. Comp. Zool., No. **251**: 1–13.

———. 1969. El primer y el cuarto grupo faunístico del Triásico de América del Sur. IV Congreso Lationoamericano de Zoología, Caracas, 1968.

———. (In press). Dos nuevas "faunas" de reptiles triásicos de Argentina. I Simposio Intern. de Estrat. y Paleont. del Gondwana, Mar del Plata, 1967.

BOONSTRA, L. D. 1953. A report on a collection of fossil reptilian bones from Tanganika Territory. Ann. South Afr. Mus., **42**: 5–18.

BRINK, A. S. 1950. Notes on a second specimen of *Homodontosaurus kitchingi*. South Afr. J. Sci., **47**: 118–119.

———. 1955. Notes on some thecodonts. Navors. Nasion. Mus. Bloemfontein, **1**(6): 141–148.

———. 1959. A new small thecodont from the Red Beds of the Stormberg Series. Palaeont. Afr., **5**: 109–115.

BROILI, F., AND J. SCHRÖDER. 1934. Beobachtungen an Wirbeltieren der Karrooformation. V. Über *Chasmatosaurus vanhoepeni* Haughton. Sitzungsber. Bayer. Akad. Wiss. München (Math.-Nat. Abt.), **1934**(3): 225–264.

BROOM, R. 1913. On the South African pseudosuchian *Euparkeria* and allied genera. Proc. Zool. Soc. London, **1913**: 619–633.

———. 1914. A new thecodont reptile. Proc. Zool. Soc. London, **1914**: 1072–1077.

———. 1922. An imperfect skeleton of *Youngina capensis* Broom in the collection of the Transvaal Museum. Ann. Transvaal Mus., **8**: 273–277.

———. 1924a. On the classification of the reptiles. Bull. Amer. Mus. Nat. Hist., **52**: 39–65.

———. 1924b. Further evidence on the structure of the Eosuchia. Bull. Amer. Mus. Nat. Hist., **51**: 67–76.

———. 1925. On the origin of lizards. Proc. Zool. Soc. London, **1925**: 1–16.

———. 1938. On a new type of primitive fossil reptile from the Upper Permian of South Africa. Proc. Zool. Soc. London, (B) **108**: 535–542.

———. 1940. Some new Karroo reptiles from the Graaff Reinet District. Ann. Transvaal Mus., **20**: 71–87.

———. 1946. A new primitive proterosuchid reptile. Ann. Transv. Mus., **20**(4): 343–346.

———. 1948. A contribution to our knowledge of vertebrates of the Karroo beds of South Africa. Trans. Roy. Soc. Edinburgh, **61**: 577–629.

———. 1949. New fossil reptilian genera from the Bernard Price collection. Ann. Transvaal Mus., **21**: 187–195.

BUNGE, M. 1959. Metascientific Queries. Springfield: Charles C. Thomas, 313 pp.

CAMP, C. L. 1930. A study of the phytosaurs. Mem. Univ. California, **10**: 1–161.

———. 1945. *Prolacerta* and the protorosaurian reptiles. Amer. J. Sci., **243**: 17–32, 84–101.

CARROLL, R. L. 1964. The earliest reptiles. J. Linn. Soc. London, **45**(304): 61–83.

CASAMIQUELA, R. M. 1961. Dos nuevos estagonolepoideos argentinos (de Ischigualasto, San Juan). Rev. Asoc. Geol. Arg., **16**(3–4): 143–203.

———. 1967. Un nuevo dinosaurio ornitisquio triásico (*Pisanosaurus mertii;* Ornithopoda) de la formación Ischigualasto, Argentina. Ameghiniana, **4**(2): 47–64.

CHARIG, A. J. 1965. Stance and gait in the archosaur reptiles. British Assoc. Adv. Sci., Ann. Meet. 1965, Sect. C, Geology, 1–7.

CHARIG, A. J., J. ATTRIDGE, AND A. W. CROMPTON. 1965. On the origin of the sauropods and the classification of the Saurischia. Proc. Linn. Soc. London, **176**(2): 197–221.

CHARIG, A. J., AND O. A. REIG. In press. The classification of the Proterosuchia.

COLBERT, E. H. 1964. Relationships of the saurischian dinosaurs. Amer. Mus. Novit., No. **2181**: 1–24.

COLBERT, E. H., AND C. C. MOOK. 1951. The ancestral crocodilian *Protosuchus*. Bull. Amer. Mus. Nat. Hist., **97**: 149–182.

COX, C. B. 1965. New Triassic dicynodonts from South America, their origins and relationships. Phil. Trans. Roy. Soc. London, (B) **248**: 457–519.

CROMPTON, A. W., AND A. J. CHARIG. 1962. A new ornithischian from the Upper Triassic of South Africa. Nature (London), **196** (4859): 1074–1077.

CROMPTON, A. W., AND M.-L. WAPENAAR (In press). Reptilian remains and trackways in

the Passage Beds (Stormberg Series of South Africa and Basutoland).

Efremov, I. A. 1938. Novye permskie reptilii SSSR. Dokl. Akad. Nauk SSSR, **19**(9): 771–776.

Ellenberger, F., and L. Ginsburg. 1966. Le gisement de dinosauriens triassiques de Maphutseng (Basutoland) et l'origine des sauropodes. C. R. Acad. Sci. Paris, (D) **262** (4): 444–447.

Ewer, R. F. 1965. The anatomy of the thecodont reptile *Euparkeria capensis* Broom. Phil. Trans. Roy. Soc. London, (B) **248**: 379–435.

Gisin, H. 1964. Synthetische Theorie der Systematik. Z. Zool. Syst. Evolutionsforsch., **2**: 1–17.

———. 1966. Signification des modalités de l'évolution pour la théorie de la systématique. Z. Zool. Syst. Evolutionsforsch., **4**(1/2): 1–12.

Goudge, T. A. 1961. The Ascent of Life. London: Allen and Unwin, 236 pp.

Gregory, J. T. 1962. The genera of phytosaurs. Amer. J. Sci., **260**: 652–690.

Haughton, S. H. 1924. The fauna and stratigraphy of the Stormberg Series. Ann. South Afr. Mus., **12**: 323–495.

Heilmann, G. 1926. The Origin of Birds. London: Witherly, 210 pp.

Hoffstetter, R. 1955. Thecodontia. *In*: J. Piveteau, ed., Traité de Paléontologie, **5**: 665–694.

Huene, F. von. 1908. Die Dinosaurier der europäischen Triasformation, mit Berücksichtigung der aussereuropäischen Vorkommnisse (part). Geol. Palaeont. Abh. Supplement-Band **1**(6): 345–419.

———. 1911. Ueber *Erythrosuchus*, Vertreter der neuen Reptil-Ordnung Pelycosimia. Geol. Palaeont. Abh., N. F., **10**: 1–60.

———. 1914a. Das natürliche System der Saurischia. Zentralbl. Min. Geol. Paläont., **1914**: 154–158.

———. 1914b. Beiträge zur Geschichte der Archosaurier. Geol. Palaeont. Abh., N. F., **13**: 1–53.

———. 1920. Osteologie von *Aëtosaurus ferratus* O. Fraas. Acta Zool., **1**: 465–491.

———. 1925. Die Bedeutung der *Sphenosuchus* Gruppe für den Ursprung der Krokodile. Z. Indukt. Abstamm. Vererbl., **38**(4): 307–320.

———. 1932. Die fossile Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. Mon. Geol. Palaeont., Ser. 1, **4**: 1–361.

———. 1938. Ein grosser Stagonolepide aus der jüngeren Trias Ostafrikas. Neues Jahrb. Min. Geol. Palaeont. Abt. B, **80**(2): 264–278.

———. 1942. Die fossilen Reptilien des Südamerikanischen Gondwanalandes. Lief. 3/4: 161–332, Munich.

———. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Jena: Gustav Fischer, 716 pp.

———. 1960. Ein grosser Pseudosuchier aus der Orenburger Trias. Palaeontographica, Abt. A, **114**(1/4): 105–111.

———. 1962. Die Pseudosuchier als Wurzelgruppe der meisten Landsaurier der Jura- und Kreidezeit. Neues Jahrb. Geol. Paläont., **1962**(1): 1–6.

Hughes, B. 1963. The earliest archosaurian reptiles. South Afr. J. Sci., **59**(5): 221–241.

Huxley, J. S. 1958. Evolutionary processes and taxonomy with special reference to grades. Uppsala Universitets Årsskrift, **6**: 21–39.

Kälin, J. 1955. Crocodilia, *In*: J. Piveteau, ed., Traité de Paléontologie, **5**: 695–784.

Krebs, B. 1963. Bau und Funktion des Tarsus eines Pseudosuchiers aus der Trias des Monte San Giorgio (Kanton Tessin, Schweiz). Paläont. Z., **37**(1/2): 88–95.

———. 1965. *Ticinosuchus ferox*, nov. gen., nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. Schweiz. Paläont. Abh., **8**: 1–140.

Kuhn, O. 1959. Die Ordnungen der fossilen "Amphibien" und "Reptilien." Neues Jahrb. Geol. Paläont., M. H., 337–347.

———. 1961. Die Familien der rezenten und fossilen Amphibien und Reptilien. Bamberg: Meisenbach K. G., 79 pp.

Kuhn-Schnyder, E. 1954. The origin of lizards. Endeavour, **13**(52): 213–219.

———. Ein weitere Schädel von *Macrocnemus bassani* Nopcsa aus der anisischen Stufe der Trias des Monte San Giorgio (Kanton Tessin, Schweiz). Paläont. Z., H. Schmidt Festband, 110–133.

———. 1963. Wege der Reptilien-Systematik. Paläont. Z., **37**(1.2): 61–87.

Lydekker, R. 1887. Note on the Hordwell and other crocodilians. Geol. Mag. (N.S.) Decade III, **4**(7): 307–312.

Mayr, E. 1965. Numerical phenetics and taxonomic theory. Syst. Zool., **14**: 73–97.

Mook, C. C. 1934. The evolution and classification of the Crocodilia. J. Geol. **42**: 295–304.

Olson, E. C. 1962. Les Problèms actuels de Paléontologie (Evolution des Vertébrés). Colloques Int. C. N. R. S., No. 104: 157–174.

———. 1965. Chickasha vertebrates. Oklahoma Geol. Surv., Circular 70: 1–70.

Parrington, F. R. 1935. On *Prolacerta broomi*, gen. et sp. nov., and the origin of lizards. Ann. Mag. Nat. Hist., Ser. 10. **16**: 197–205.

———. 1956. A problematic reptile from the Upper Permian. Ann. Mag. Nat. Hist., Ser. 12, **9**: 333–336.

———. 1958. The problem of the classification

of reptiles. J. Linn. Soc. London, Zool., **44** (295): 99–115.

PEABODY, F. E. 1948. Reptile and amphibian trackways from the Lower Triassic Moenkopi Formation of Arizona and Utah. Univ. Calif. Publ. Bull. Dept. Geol. Sci., **27**(8): 295–468.

———. 1952. *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas. Univ. Kansas Paleont. Contrib., Vertebrata, **1**: 1–41.

———. 1955. Occurrence of *Chirotherium* in South America. Bull. Geol. Soc. Amer., **66**: 239–240.

PEARSON, H. S. 1924. A dicynodont reptile reconstructed. Proc. Zool. Soc. London, **1924**: 827–855.

PIVETEAU, J. 1955. Eosuchia. *In*: J. Piveteau, ed., Traité de Paléontologie, **5**: 545–557.

POPPER, K. R. 1959. The Logic of Scientific Discovery. London: Hutchinson, 480 pp.

PRICE, L. I. 1946. Sôbre um novo pseudosuquio do Triásico superior do Rio Grande do Sul. Minist. Agric. Div. Geol. Min., Bol. **120**: 1–38.

REIG, O. A. 1959. Primeros datos descriptivos sobre nuevos reptiles arcosaurios del Triásico de Ischigualasto. Rev. Asoc. Geol. Arg., **13** (4):257–270.

———. 1961. Acerca de la posición sistemática de la familia Rauisuchidae y del género *Saurosuchus* (Reptilia, Thecodontia). Publ. Mus. Munic. Cien. Nat. Trad. Mar de Plata, **1**(3): 73–114.

———. 1963a. La presencia de dinosaurios saurisquios en los "Estratos de Ischigualasto" (Mesotriásico superior) de las provincias de San Juan y La Riojo (República Argentina). Ameghiniana, **3**(1): 3–20.

———. 1963b. Anagenesis and the processes of evolutionary progress. Proc. XVI Internat. Cong. Zool., Washington, D. C., August 20–27, 1963, Vol. **2**: 185.

———. 1967. Archosaurian reptiles: a new hypothesis on their origins. Science, **157**: 565–568.

———. 1968. Los conceptos de especie en la biología. Ediciones Biblioteca Univ. Central de Venezuela. Caracas, 43 pp.

RENSCH, B. 1947. Neuere Probleme der Abstammungslehre: die transspezifische Evolution. Stuttgart: Enke, 407 pp.

ROMER, A. S. 1945. Vertebrate Paleontology. 2nd ed. Chicago: Univ. Chicago Press, 687 pp.

———. 1946. The primitive reptile *Limnoscelis* restudied. Amer. J. Sci., **244**: 149–188.

———. 1956. Osteology of the Reptiles. Chicago: Univ. Chicago Press, 772 pp.

———. 1966a. The Chañares (Argentina) Triassic reptile fauna. I. Introduction. Breviora, Mus. Comp. Zool., No. **247**: 1–14.

———. 1966b. Vertebrate Paleontology. 3rd ed., Chicago: Univ. Chicago Press, 468 pp.

———. 1967. Early reptilian evolution reviewed. Evolution, **21**: 821–833.

———. In press. Middle Triassic tetrapod faunas of South America. IV Congreso Latinoamericano de Zoología, Caracas, 1968.

ROMER, A. S., AND L. I. PRICE. 1940. Review of Pelycosauria. Geol. Soc. Amer. Spec. Pap., No. **28**: 1–538.

ROZHDESTVENSKII, A. K. 1964. Klass Reptilia. Reptilii, ili presmykaiushtchiesia. Obshtchaia chast. *In*: J. A. Orlov, ed., Osnovy Paleontologii. Zemnovodnye, presmykaiushtchiesia i ptitzy. Moscow, pp. 191–213.

RUSCONI, C. 1951. Laberintodontes triásicos y pérmicos de Mendoza. Rev. Mus. Hist. Nat. Mendoza, **5**: 33–158.

SATSANGI, P. P. 1964. A note on *Chasmatosaurus* from the Panchet series of Raniganj coalfield, India. Current Sci., **33**(21): 651–652.

SAWIN, H. J. 1947. The pseudosuchian reptile *Typothorax meadei*. J. Paleont., **21**: 201–238.

SCHMIDT-NIELSEN, K. 1958. Salt glands in marine reptiles. Nature (London), **182**(4638): 783–785.

SHAROV, A. G. 1965. Evolution and taxonomy. Z. Zool. Syst. Evol.-forsch. **3**(3/4): 349–358.

SILL, W. 1967. *Proterochampsa barrionuevoi* and the early evolution of the Crocodilia. Bull. Mus. Comp. Zool., **135**: 415–446.

SIMPSON, G. G. 1953. The Major Features of Evolution. New York: Columbia Univ. Press, 434 pp.

———. 1959. The nature and origin of supraspecific taxa. Cold Spring Harbor Symp. Quant. Biol., **24**: 255–271.

———. 1961. Principles of Animal Taxonomy. New York: Columbia Univ. Press, 247 pp.

SNEATH, P. H. A. 1962. The construction of taxonomic groups. *In*: G. C. Ainsworth and P. H. A. Sneath, eds., Microbial Classification. Cambridge: Cambridge Univ. Press, pp. 289–332.

SOKAL, R. R., AND P. H. A. SNEATH. 1963. Principles of Numerical Taxonomy. San Francisco and London: Freeman and Co., 359 pp.

SUN, A. L. 1963. The Chinese kannemeyerids. Paleont. Sinica, (C) **17**:1–109.

TAKHTAJAN, A. 1959. Die Evolution der Angiospermen. Jena: Gustav Fischer.

TATARINOV, L. P. 1959. Proishkhozhdenie presmykaiushtchiesia i nekotorye printzipy ikh klassifikatzii. Paleont. Zh. 1959, **4**: 65–84.

———. 1961. Materialy po psevdozukhiian S.S.S.R. Paleont. Zh. 1961, **1**: 117–132.

———. 1964. Otriad Millerosauria. *In*: J. A. Orlov, ed., Osnovy Paleontologii: Zemnovodnye,

presmykaiushtchiesia i ptitzy. Moscow, pp. 444–446.

Templeton, J. R. 1964. Nasal salt excretion in terrestrial lizards. Comp. Biochem. Physiol., **11**: 223–229.

———. 1966. Responses of the lizard nasal salt gland to chronic hypersalemia. Comp. Biochem. Physiol., **18**: 563–572.

Vaughn, P. P. 1955. The Permian reptile *Araeoscelis* restudied. Bull. Mus. Comp. Zool., **113**: 305–467.

Versluys, J. 1910. Streptostylie bei Dinosaurien, nebst Bemerkungen über die Verwandtschaft der Vögel und Dinosaurier. Zool. Jahrb., Abt. Anat., **30**(2): 175–260.

———. 1912. Das Streptostylie-Problem und die Bewegungen im Schädel bei Sauropsiden. Zool. Jahrb. Suppl. XV (Festschrift J. W. Spengel), 2: 545–716.

Waddington, C. H. 1960. The Ethical Animal. London: Allen and Unwin, 230 pp.

Walker, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. Phil. Trans. Roy. Soc. London, (B) **244**: 103–204.

———. 1964. Triassic reptiles from the Elgin area: *Ornithosuchus* and the origin of carnosaurs. Phil. Trans. Roy. Soc. London, (B) **248**: 53–134.

———. 1966. *Elachistosuchus*, a Triassic rhynchocephalian from Germany. Nature (London), **211**: 583–585.

———. 1968. *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodiles. Geol. Mag. **105**(1): 1–14.

Watson, D. M. S. 1954. On *Bolosaurus* and the origin and classification of reptiles. Bull. Mus. Comp. Zool., **111**: 297–449.

———. 1957. On *Millerosaurus* and the early history of the sauropsid reptiles. Phil. Trans. Roy. Soc. London, (B) **240**: 325–400.

———. 1960. The anomodont skeleton. Trans. Zool. Soc. London, **29**(3): 131–208.

———. 1962. The evolution of the labyrinthodonts. Phil. Trans. Roy. Soc. London, (B) **245**: 219–265.

Williston, S. W. 1914. The osteology of some American Permian vertebrates, I. Contrib. Walker Mus., **1**: 107–182.

Wilson, E. O. 1965. A consistency test for phylogenies based on contemporaneous species. Syst. Zool., **14**: 214–220.

Woodger, J. H. 1952. Biology and Language. Cambridge: Cambridge Univ. Press, 364 pp.

Young, C. C. 1936. On a new *Chasmatosaurus* from Sinkiang. Bull. Geol. Soc. China, **15** (3): 291–311.

———. 1963. Additional remains of *Chasmatosaurus yuani* Young, from Sinkiang, China. Vertebr. Palas. **7**(3): 215–222.

———. 1964. The pseudosuchians in China. Paleont. Sinica, (Ser. C) **19**: 1–205.

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ADDENDUM

After this paper was submitted for publication, some important contributions appeared that are relevant to several of the topics herein discussed.

The question of crocodile origins and the evolutionary meaning of *Proterochampsa* merited a paper by Walker (1968) that introduced radical changes in previous interpretations, including the views sustained in this paper. Walker affords a new look at the cranial structure of *Stegomosuchus* on the basis of casts procured by Dr. Romer, which allowed him to reinterpret the roof of the skull of *Protosuchus* as known from the photographs given by Colbert and Mook (1951). On the basis of these new interpretations, and of similarities in the dermal scutes, Walker concluded that *Stegomosuchus* is closely related to *Protosuchus*, and even that *Stegomosuchus longipes* could be a juvenile of *Protosuchus richardsoni*. Furthermore, in his view, the skull of *Protosuchus* indicates that this genus is much more closely related to *Notochamsa* than was previously maintained. Thus, his conclusion is that these three genera are to be placed in a single family of the suborder Protosuchia of crocodiles, a family that, by priority, should be named Stegomosuchidae.

Although I accept that some of these views might be proved as well substantiated by further work on the actual specimens of these forms, I hardly think it justified to propose such drastic changes without observing the original specimens. The same criticism applies to Walker's reappraisal of the phylogenetic place of *Proterochampsa*.

Walker analyzed 16 characters, most of which would afford "ample evidence for regarding *Proterochampsa* as a very primitive phytosaur, and not a crocodile" (1968:

11). This conclusion is, of course, of great interest, but here again the foundations might be suspected, due to the lack of direct observations of the several available specimens of the discussed genus. Moreover, Walker bases a part of his argument on my first description of *Proterochampsa* (Reig, 1959), a description which has been corrected by Sill's work (1967), based on broader comparisons and on more specimens, some of them better preserved.

There is not the space here to attempt a thorough discussion of Walker's arguments on the place of *Proterochampsa*. I wish to advance, however, my feeling that several parts of his analysis deserve serious consideration and a careful checking in the light of the actual specimens. Nevertheless, I am strongly convinced that, until this work is accomplished, it is wiser to maintain Sill's interpretation of *Proterochampsa* as the correct one, as, furthermore, it is the only one which is based on direct comparisons.

Another interesting suggestion in Walker's paper is his belief that *Cerritosaurus* (here considered as a probable junior synonym of *Rhadinosuchus*) possesses "some at least of the attributes one expects to find in a crocodile ancestor" (Walker, 1968: 11–12). We have already mentioned the isolated position of this genus among the Pseudosuchia, and the difficulties that arise in tracing its origins from the early and central Pseudosuchian family Euparkeriidae. Thus, Walker's suggestion seems to deserve serious consideration here, as it is likely to make more balanced the phylogenetic scheme of the Pseudosuchia.

Needless to say, new evidence might also be critical for the testing of Walker's views, and this evidence may already be available through Romer's and Bonaparte's new findings in the pre-Ischigualasto Chañares formation of La Rioja (Romer, 1966a, and *in press*). These two colleagues found excellent specimens of a small archosaurian showing significant resemblances to *Proterochampsa* (Romer and Bonaparte, pers. comm.). The animal, still undescribed, could be the key to the correct interpretation of *Proterochampsa* and other early crocodiloid forms, including the awkward *"Cerritosaurus."*

Furthermore, new light on the question of early crocodilian history will surely be shed by Bonaparte's recent findings in the Upper Triassic Los Colorados Beds of Ischigualasto (Bonaparte, 1969, in press.). These findings, still mostly undescribed, include two crocodiloid archosaurians. One of them is closely related to *Sphenosuchus* and *Hesperosuchus*, the other resembles *Protosuchus*. The former is also related to *Triassolestes romeri* from the Ischigualasto beds, an archosaur which I described (Reig, 1963) as a saurischian dinosaur. In that paper, I tentatively referred to *Proterochampsa* a fore-limb showing the typical carpal structure of crocodiles associated with the type skull of *Triassolestes romeri*. Now, the *Sphenosuchus*-like new archosaurian from Los Colorados found by Bonaparte (Pers. comm. and 1969), which include both cranial and postcranial material, allowed him to conclude that the fore-limb associated with *Triassolestes*' skull actually belongs to the same individual represented by the skull. *Triassolestes* is to be interpreted, therefore, as a primitive crocodilian of the group of "dinosaur-like crocodiles."

In all likelihood, after these new findings of the Argentinian Middle and Upper Triassic are described, we shall have a better understanding of the various crocodiloid forms currently classified as Protosuchids, Notochampsids, Sphenosuchids, etc. We can suppose, therefore, that a new appraisal of early crocodilian history will come in the near future.

A recent description of ornithischian dinosaur remains from the Ischigualasto beds (Casamiquela, 1967) makes it necessary to change some of the tentative conclusions of previous pages on the time of origin of this taxon. Although the new

findings, described as *Pisanosaurus mertii*, are too fragmentary to afford precise observations on the problem of Ornithischian ancestry, they are conclusive first of all in proving the presence of a full-fledged ornithopod in the upper Middle Triassic of Argentina, and secondly, in tracing the origin of ornithischian dinosaurs well into the early Middle Triassic, that is to say, at the very beginning of the first diversification of the non-proterosuchian archosaurs.

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New Fossil Pelobatid Frogs and a Review of the Genus *Eopelobates*

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NEW FOSSIL PELOBATID FROGS AND A REVIEW OF THE GENUS *EOPELOBATES*

RICHARD ESTES[1]

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ABSTRACT

Eopelobates was a fossil pelobatid frog that lived in North America during the Eocene and early Oligocene, and may have been present in the Cretaceous as well. In Europe, it extended from middle Eocene through the middle Miocene. In many ways *Eopelobates* is intermediate between megophryine and pelobatine subfamilies, but is retained here in the Megophryinae because of absence of an enlarged prehallux, or spade. Two lines may be distinguished within the genus: a primitive, short-skulled group composed of the North American *E. guthriei* n. sp. and *E. grandis*, with the European *E. anthracinus* probably included here as well, and a long-skulled European lineage composed of *E. hinschei* (n. comb.) and *E. bayeri*.

The spadefoot toads were probably derived from *Eopelobates*, and the primitive *E. guthriei* shows some indications of spadefoot relationship. The earliest true spadefoot was *Scaphiopus skinneri* n. sp., from the early and middle Oligocene of North America. It has some primitive features but is already close to the modern *S. holbrooki*. A form close to *Pelobates* was also present in the early Oligocene of Europe, further implying at least an Eocene divergence of the spadefoots from the megophryines. The early or middle Oligocene *Macropelobates* from Mongolia links *Eopelobates* and the spadefoots in some

features, but the contemporaneous record of *Scaphiopus* described here indicates that it was too late to have been ancestral to the modern subfamily. *Macropelobates* is best interpreted as a relict of the spadefoot group that gave rise to both *Scaphiopus* and *Pelobates*. It seems to be most closely related to the primitive modern species *P. cultripes*, and also shows some similarity to the primitive *S. skinneri*. *Miopelobates*, a primitive pelobatine that lived in Europe in the middle Miocene and early Pliocene, may have been an early offshoot from the ancestral spadefoot.

The modern megophryines are tropical and subtropical and probably diverged from an *Eopelobates*-like form no later than the Cretaceous. *Leptobrachium* is the most primitive of the modern megophryines and is in some ways the most *Eopelobates*-like of the group. Megophryines of modern type were probably restricted to the southern part of the Eurasian continent during the early Cenozoic; they have undergone a separate radiation and have developed both high- and low-altitude terrestrial forms from the more aquatic, primitive types.

The Pelobatidae probably differentiated from a discoglossid-like ancestor in the Holarctic middle-latitude tropics, and the primitive aquatic megophryine *Eopelobates* gave rise to the terrestrial spadefoots in response to early Cenozoic climatic deterioration in both Europe and North America. Similarities between the two modern pelobatines indicate that they probably had a common ancestry.

INTRODUCTION AND ACKNOWLEDGMENTS

Although fossil frogs are relatively rare, the pelobatid frogs are one of the most frequently encountered frog families in the Cenozoic fossil record, especially in the Oligocene and Miocene. Many different forms have been described from North American late Cenozoic deposits and have been recently reviewed by Kluge (1966) and Zweifel (1956). I am principally concerned here with the Eocene, Oligocene, and early Miocene forms and describe two new fossil finds that bear on the evolution of the Pelobatidae: (1) an early Eocene skull of *Eopelobates* from Wyoming, and (2) a skull and partial skeleton of a primitive *Scaphiopus* from the middle Oligocene of North Dakota.

I am especially grateful to Professor Zdeněk Špinar for discussion, for providing measurements, and for allowing me to utilize his new specimen of *Eopelobates bayeri* in this study. I also thank Dr. Alan Charig of the British Museum (Natural History); Dr. R. Hoffstetter (Muséum National d'Histoire Naturelle, Paris); Dr. H. Matthes (Geologisch-Paläontologisches Institut, Martin Luther University, Halle); Dr. H. Zapfe (Universität Wien); Dr. Donald Baird (Princeton University); Dr. Max Hecht (Queens University, N. Y.); and Dr. Arnold Kluge (University of Michigan) for allowing me to study specimens in their care. Dr. Daniel Guthrie (Pfitzer College, California) and Mr. Morris Skinner (Frick Laboratory, American Museum of Natural History) deserve special thanks for providing the new *Eopelobates* and *Scaphiopus* material described here. Mr. Walter P. Murphy, Jr. aided in the description of the latter as part of an Honors Program project in Biology, Boston University.

Drs. Špinar, Hecht, Ernest Williams (Harvard University), Charles Meszoely (Northeastern University), and J. A. Tihen (Notre Dame University) have offered helpful comments on the manuscript. Mr. Fred Maynard prepared Figures 14 and 30; Mrs. Patricia Kerfoot drew Figures 29 and 30.

This study was supported in part by National Science Foundation Grant GB-4303.

Abbreviations

AM = American Museum of Natural History, New York City.

BM = British Museum (Natural History), London.
CUPI = Charles University Paleontological Institute, Prague.
FAM = Frick Laboratory, American Museum of Natural History, New York.
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge.
MME = Museum für Mitteldeutsche Erdgeschichte, Geologisch-Paläontologisches Institut, Halle (Saale).
PU = Princeton University Museum of Geology, Princeton.
UCMP = University of California Museum of Paleontology, Berkeley.
UMMZ = University of Michigan Museum of Zoology, Ann Arbor.

THE STATUS OF THE GENUS EOPELOBATES

Eopelobates anthracinus Parker (1929) is from the lignite beds of Rott, near Bonn, Germany. It lacks a spade (Fig. 1) and is unlikely to have been fossorial. Parker called the beds Lower Miocene, but Westphal (1958) states them to be middle Oligocene (Rupelian). Špinar (1952) noted the presence of a larger, related species, *E. bayeri*, from Bechlejovice, near Děčin, Czechoslovakia, in beds of Chattian or Aquitanian age (late Oligocene or early Miocene). The presence of a spade was not determinable in his specimen. Hecht (1963, p. 23) suggested that *E. bayeri* was in fact referable to *Pelobates*. Zweifel (1956) referred a spadeless early Oligocene specimen from the Chadron Formation of South Dakota to a new species, *E. grandis*.

I have recently examined all published material of *Eopelobates* and have also had the privilege of studying both a new complete specimen of *E. bayeri* and an associated series of tadpoles of this species collected by Professor Špinar. He will describe these in detail but he has kindly allowed me to figure (Fig. 2) and briefly discuss the adult animal in order to justify the generic assignment.

Except in a few cases in which the nature of the specimen precludes knowledge, material referred to *Eopelobates* shows the following features: (1) prominent, elongated sternal style; (2) strong posterior projection of the ischium; (3) spade absent; (4) long, relatively slender limbs; (5) urostyle either separate, partially, or completely fused with sacrum; (6) sacral diapophyses strongly dilated; (7) tibia longer than femur; (8) approximately subequal orbit and temporal openings; (9) dermal ossification well developed and fused to skull roof; (10) skull roof flat or concave dorsally; (11) ethmoid wide and blunt anteriorly, and with dorsal ethmoid roof over nasal capsules; (12) squamosal-frontoparietal connection absent; (13) prominent, well-ossified paroccipital processes on frontoparietal and occiput; (14) complete maxillary arcade; (15) femur-tibia length approaching or exceeding head-body length. Comparison with the two currently recognized subfamilies of pelobatids, the Pelobatinae and Megophryinae, indicates similarity of *Eopelobates* to both groups. The most clearcut megophryine resemblances are 2, 3, 4, 7, 8, 10, and 11. The only specific pelobatine feature is 9, but in a number of other features discussed below *Eopelobates* shows pelobatine resemblances. In 1, 6, 13, and 14 resemblance to both groups occurs. Character 5 is variable and useless as Zweifel (1956, p. 12) has suggested.

I believe that *in combination* characters 3, 7, 9, 10, 11, 12, and 15 validate *Eopelobates* as a distinct genus. In many ways, *Eopelobates* is intermediate between the two Recent subfamilies; this relationship will be discussed later in this paper. Zweifel's characterization of the genus (1956, p. 13) as extremely close to *Megophrys* is still valid, but it requires qualification. Hecht's contention (based only on the type) that *Eopelobates bayeri* is a

Figure 1. *Eopelobates anthracinus*, BM R-4841; × 3.

Pelobates is not supported by the new, complete specimen. There are indications, however, that an *Eopelobates*-like form gave rise to the spadefoot toads; these indications will be discussed below in the section on *Scaphiopus* and the new species of *Eopelobates* from Wyoming.

Following Zweifel (1956), a revised diagnosis of *Eopelobates* might read: pelobatid frogs with a fused encrustation

Figure 2. *Eopelobates bayeri*, CUPI 6.874; × 1. Left, 6.874a, imprint of ventral surface; right, 6.874b, counterpart, imprint of dorsal surface.

of dermal bone on the skull; skull roof concave or flattened medially; maxillary teeth present; eight procoelous presacral vertebrae; sacral diapophyses widely expanded; squamosal in wide contact with maxilla; no squamosal-frontoparietal contact; no bony prehallux or spade; tibia longer than femur; combined femur-tibiofibula length more than 90% of length from anterior tip of skull to tip of urostyle. This diagnosis differs from that of Zweifel in several respects. First, there is no frontoparietal-squamosal bar in *Eopelobates,* contrary to statements in the literature (see below under *E. grandis* and *E. anthracinus*). The term "postorbital bar" is confusing, since there is a possibility of "postorbital" contact both between maxilla and squamosal and between squamosal and frontoparietal. Neither Zweifel nor Parker were always specific in referring to this matter. Second, all species have a tibia either slightly or substantially longer than femur. Third, Zweifel (1956, p. 12) states that tibia and femur are "together somewhat shorter than the head-body length"; this is true of all Recent or fossil pelobatids measured by me, with the exception of *E. bayeri* and *E. hinschei* (see below).

The Family Assignment of Eopelobates

This has been discussed by Zweifel (1956). In the combination of procoelous vertebrae, imbricate neural arches, probable arciferal pectoral girdle, single coccygeal condyle, prominent sternal style, wide dilation of sacral diapophyses, long anterior and short posterior transverse processes, and the general aspect of the skull and skeleton, *Eopelobates* is referable to the Pelobatidae without much question.

Discussion of Anatomical Features

Before discussing the individual species of *Eopelobates,* a brief evaluation of selected anatomical features is necessary. Little or no attention will be given to features that have been treated adequately elsewhere or are not applicable to fossils.

Frontoparietal-Squamosal connection

Mertens (1923) believed *Pelobates fuscus* to be primitive because of the ligamentary frontoparietal-squamosal connection. Such a connection is not constant in either *P. cultripes* or *P. syriacus.* There is interpopulational variation as indicated by Başoğlu and Zaloğlu (1964; see also Fig. 27, this paper) and the connection may be absent in small individuals of *P. cultripes* (MCZ 15376). In most Recent megophryines, except *Leptobrachium hasselti* and *Scutiger mammatus,* a specialized connection of frontoparietal and squamosal occurs on the surface of the prootic, ventral to the temporal musculature (Fig. 11d).

Absence of the superficial, sculptured frontoparietal-squamosal connection in both *Eopelobates* and the Oligocene pelobatine *Macropelobates* probably indicates the primitive pelobatine condition. I believe, however, that Gislén (1936) was correct in suggesting that *Pelobates cultripes* is primitive, although my reasons for this decision are different from his (see section below on *Pelobates*).

In *Megophrys,* dermal ossification spans frontoparietal and squamosal, and Zweifel (1956, p. 15) has suggested that the presence of considerable dermal bone may be a primitive condition. While it is true that a complete bony head casque may develop in large individuals of *Megophrys carinensis, M. monticola,* and perhaps other species, this is not fused to the skull bones, but instead coalesces from peculiar, irregular dermal plaques that usually remain separate, even though they grow to meet each other. Dermal covering lacks discrete boundaries and may extend into the skin of the dorsum; it is therefore quite different from the sculptured, fused, and discrete ossifications of pelobatines and *Eopelobates.* Whether it is an independently derived condition or a degeneration from a fused, *Eopelobates*-like condition cannot be determined. Many fossil frogs have

secondary dermal sculpture on the skull roof, and these forms occur as far back as the late Jurassic; some other Jurassic frogs, however, lack dermal sculpture. Extensive dermal skull sculpture is present in some Hylidae, Leptodactylidae, Ranidae, Bufonidae, Rhacophoridae, and Discoglossidae; most of these groups have acquired this dermal covering independently.

Prootic Foramen

Kluge (1966, p. 13) has shown some apparent morphogenetic trends in the shape of the prootic foramen (= trigeminal foramen). There is a tendency for this to be surrounded by bone in some species, but in general, the foramen is open anteriorly (e.g. in *Megophrys* and in *Pelobates cultripes*). The foramen is narrow in both *Scaphiopus* (*Scaphiopus*) and the one species of *Eopelobates* in which this is known (*E. guthriei* n. sp.; see p. 309). In *Pelobates fuscus,* this foramen is elongated vertically and in some specimens may be surrounded by bone, as in *Scaphiopus* (*Spea*).

While a trend toward closure does seem to exist, this is quite variable throughout the pelobatid series, as might be imagined in a condition involving minor degrees of ossification. The actual shape variation is even greater within species than Kluge indicated (Fig. 16). Care should be taken in the use of this character. Study of the soft structures involved would be useful, as would a functional study of the correlation of closure of foramen with the loss of dermal roofing bone.

Orbitotemporal Opening

The proportions of orbit and temporal opening vary widely in pelobatids (Fig. 15). In *Megophrys* and *Eopelobates,* the skull is relatively broad and flat and the orbito-temporal openings are of about equal size. In pelobatines there is a tendency towards the enlargement of the orbit and the reduction of the temporal area and rear part of skull. This is most extreme in *Scaphiopus couchi* and *S.* (*Spea*), and results in a major change in the squamosal angle (see below and Figs. 15, 17). Other skull changes accompany this one and result in the high, domed, toad-like skull of these species.

Squamosal Angle

Griffiths (1963, p. 248) gave three categories for the condition of the angle between squamosal and quadratojugal, and for the origin of the depressor mandibulae: (1) depressor mandibulae originating from the squamosal stem and otic arm; squamosal angle > than 55° (Bufonidae, Brachycephalidae); (2) muscle originating from squamosal and dorsal fascia, squamosal angle 45°–50° (Ranidae, Microhylidae, Rhacophoridae, Leptodactylidae, Hylidae); (3) muscle originating only from dorsal fascia, squamosal angle < 45° (Discoglossidae, Pelobatidae). He noted that all groups passed through condition (1) in their development and that care should be taken in using this character because of the possibility of parallel paedomorphy.

In specimens I measured, the squamosal angle was 45° or less only in *Megophrys;* but in *Eopelobates guthriei* nov. (see below), *E. hinschei,* and *Scaphiopus skinneri* nov. (see below), the angle fell between 45° and 50°. All other pelobatines were between 56° and 73°, the highest in *S. couchi.* This change in the squamosal angle suggests that the development of a higher skull and larger orbit in pelobatines (discussed above) may involve a paedomorphic trend.

Ossified Sternum

Kluge (1966, p. 17) noted that Griffiths (1963, p. 271) was incorrect in stating that all pelobatids have an ossified sternal apparatus. Zweifel (1956, p. 24) states that the sternum is cartilaginous in *Scaphiopus.* This seems to be true in general, but a specimen of *S. couchi* chosen at random

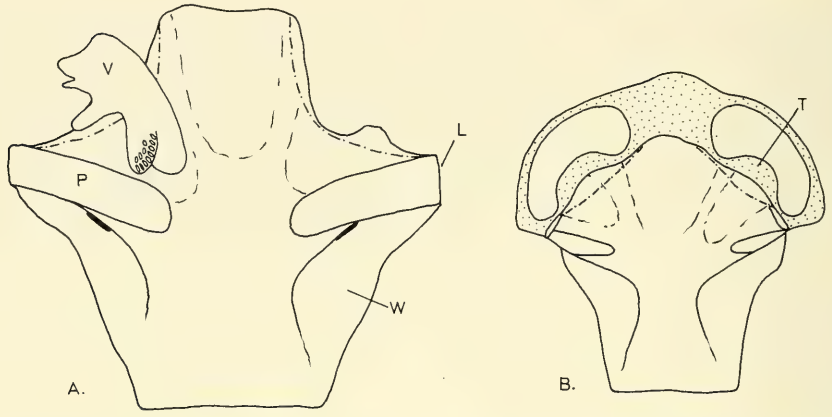

Figure 3. (A) *Megophrys carinensis*, AM 23965, ventral view of ethmoid and vomer; (B) *Megophrys robusta*, MCZ 25735, ventral view of ethmoid, ethmoid cartilage stippled; both × 3. —.—.—.—.— = dorsal border of ethmoid roof; L = lateral process; P = palatine articulation surface; T = turbinal fold in cartilage; V = vomer; W = lateral wing.

(MCZ 64374, cleared and stained) has an irregular sternal ossification (Fig. 9d) in the stylar region, and an ossified, paired omosternum as well. Although this condition has not yet been described in a fossil *Scaphiopus* and I have not checked it in *S. holbrooki*, it is possible that some ossification is the primitive condition in *Scaphiopus*.

Ethmoid

The ethmoid shows considerable intergeneric variation in general shape, and since it is often found in fossils it can be useful in identification. I lack sufficient material for a meaningful study on intrageneric variation, but the material available seems to be relatively consistent and to demonstrate that some species may be identifiable on this basis as well.

In *Megophrys* the ethmoid is pinched-in ventrally, but develops lateral wings dorsally, giving a rhombic shape to the dorsal surface of the bone. In *Leptobrachium* no lateral wings are present and the ethmoid is hour-glass shaped. The lateral processes (Fig. 3) are prominent, but are not strongly separated from the anterior process by emargination in the choanal region. The palatines underlie the lateral processes and the vomers lie along the lateral sides of the anterior process. Internally there is only a faint development of a turbinal fold between lateral and anterior processes, if it is present at all (Fig. 4); however, a turbinal fold is present in cartilage. The internal surface is flattened dorsoventrally and the capsule area is completely roofed by the ethmoid; only at the anterior end is it covered by the nasal. In *Pelobates cultripes* and *P. syriacus*, the anterior process is moderately developed, but the end of the process is relatively blunt with only a slight median projection. The turbinal fold is moderately developed.

In *Pelobates fuscus* and especially in *Scaphiopus*, there is marked separation of the anterior and lateral processes by emargination. In the emarginated area between those processes, *P. fuscus* has a moderately developed turbinal fold, and *Scaphiopus* a very well developed one. In both species (except *S. holbrooki*), the turbinal fold projects strongly in ventral view as the capsular process (Fig. 5), and the anterior process itself has two separate projections. The capsular process is much better developed in *Scaphiopus* (again,

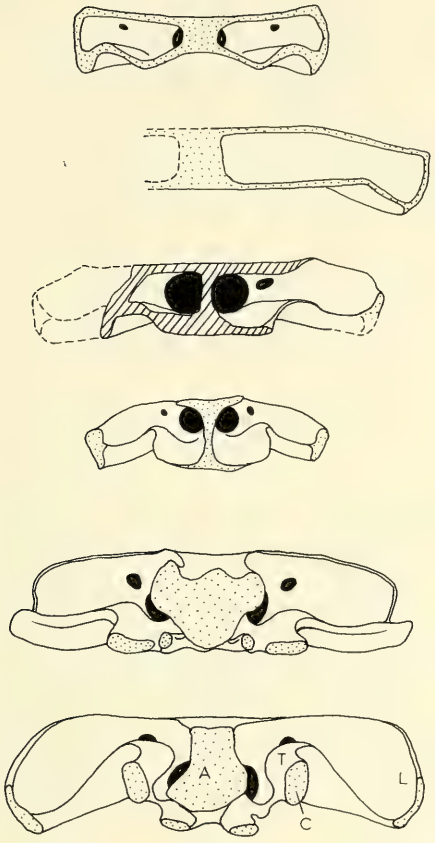

Figure 4. Ethmoids in anterior view; *a, Megophrys monticola*, AM 23964; *b, Eopelobates grandis*, PU 16441; *c, Macropelobates osborni*, AM 6252; *d, Pelobates cultripes*, UMMZ S-2630; *e, Pelobates fuscus*, MCZ 1012; *f, Scaphiopus couchi*, AM 56284; *a–d*, × 3; *e–f*, × 6; diagonal hatching = broken surface, dashed line = restoration, stippled area = cartilage attachment surface; A = anterior process; C = capsular process; L = lateral process; T = turbinal fold.

except in *S. holbrooki*) and is somewhat different than in *Pelobates fuscus*.

In *Eopelobates* intermediate conditions prevail, so far as this can be determined in the fossil material. There is definite separation of lateral and anterior processes by emargination in *E. bayeri*, although the general configuration is more *Megophrys*-like than pelobatine. The anterior process as shown in *E. guthriei* n. sp. and *E. bayeri* ossifies very little (see p. 312 and Fig. 6), and remains broad as in megophryines.

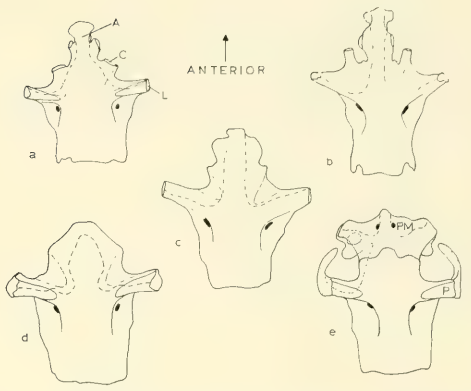

Figure 5. Pelobatine ethmoids in ventral view; *a, Pelobates fuscus*, MCZ 1012; b, *Scaphiopus couchi*, AMNH 56284; *c, S. holbrooki*, MCZ 25577; *d, P. cultripes*, UMMZ S-2730; *e, P. varaldii*, MCZ 31970, with ethmoid cartilage in stipple; all × 2. Irregular line = depression; — . — . — . — . — = dorsal border of bony ethmoid; — — . — — . — — = dorsal border of ethmoid cartilage. A = anterior process; C = capsular process; L = lateral process; P = palatine articulation surface; PM = premaxillary articulating surface.

This situation is approached in *P. varaldii* (separated from *P. cultripes* by Pasteur and Bons, 1959; Fig. 5e, this paper). A separate anterior process is not present on *E. grandis* (Fig. 7) and is not visible in the other species. In the ventral view of *E. bayeri*, a depression develops between lateral and anterior processes, reflecting a weak turbinal fold development like that of *Megophrys* and *Pelobates*, but not as distinct as in *Scaphiopus*. The ethmoid of *Macropelobates* is as in *P. cultripes*, as far as can be determined (*cf.* Figs. 7b; 5d).

In all pelobatines, the dorsal ethmoid roof of the nasal capsule is absent and the entire capsule is then roofed by the nasal (Fig. 5), but in *Megophrys* the ethmoid floor and roof are of about equal extent and the nasal provides cover for the capsules only anteriorly (Fig. 7). The extent of roofing by ethmoid in *Eopelobates* can be seen only in *E. grandis*, and is approximately as in the megophryines. In the subgenus *Spea* of *Scaphiopus*, the anterior process may become extremely large and

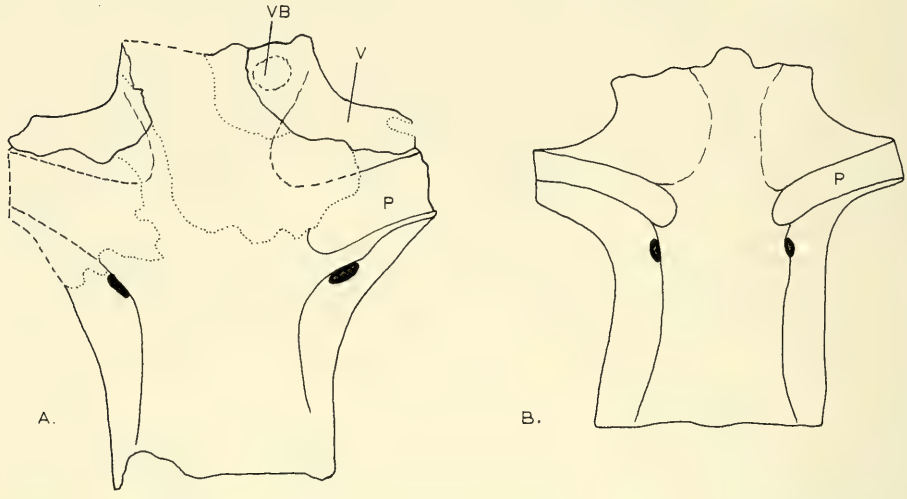

Figure 6. Ventral view of ethmoid of (A) *Eopelobates guthriei*, MCZ 3493, × 3; (B) *E. bayeri*, CUPI 6.874, × 5.5. Dashed line = restoration, dotted line = broken bone outline; P = palatine articulation; VB = boss for vomerine teeth.

flared anteriorly (e.g. *S. intermontanus*), producing the most extreme pelobatine condition.

The bony ethmoid is, of course, merely an ossified portion of the ethmoid cartilage and not coextensive with it. The cartilage itself is also quite different in the two modern subfamilies (cf. Figs. 3b, 5e) and within that cartilage, the above-noted variations in ossification occur. The retreat of the bony roof of the pelobatine ethmoid is accompanied by regression of the cartilage to a partial ring surrounding the naris and a thin, membranous cover over the main unossified part of the capsule.

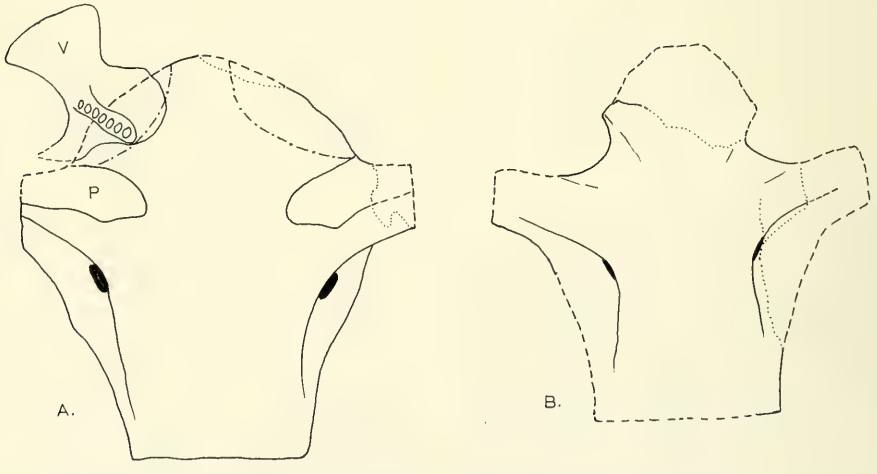

Figure 7. (A) *Eopelobates grandis*, PU 16441, ventral view of ethmoid and vomer; (B) *Macropelobates osborni*, AM 6252, ventral view of ethmoid; both × 3. Dashed line = restoration; dotted line = broken bone surface; — . — . — . — = dorsal border of ethmoid; V = vomer; P = palatine articulation surface.

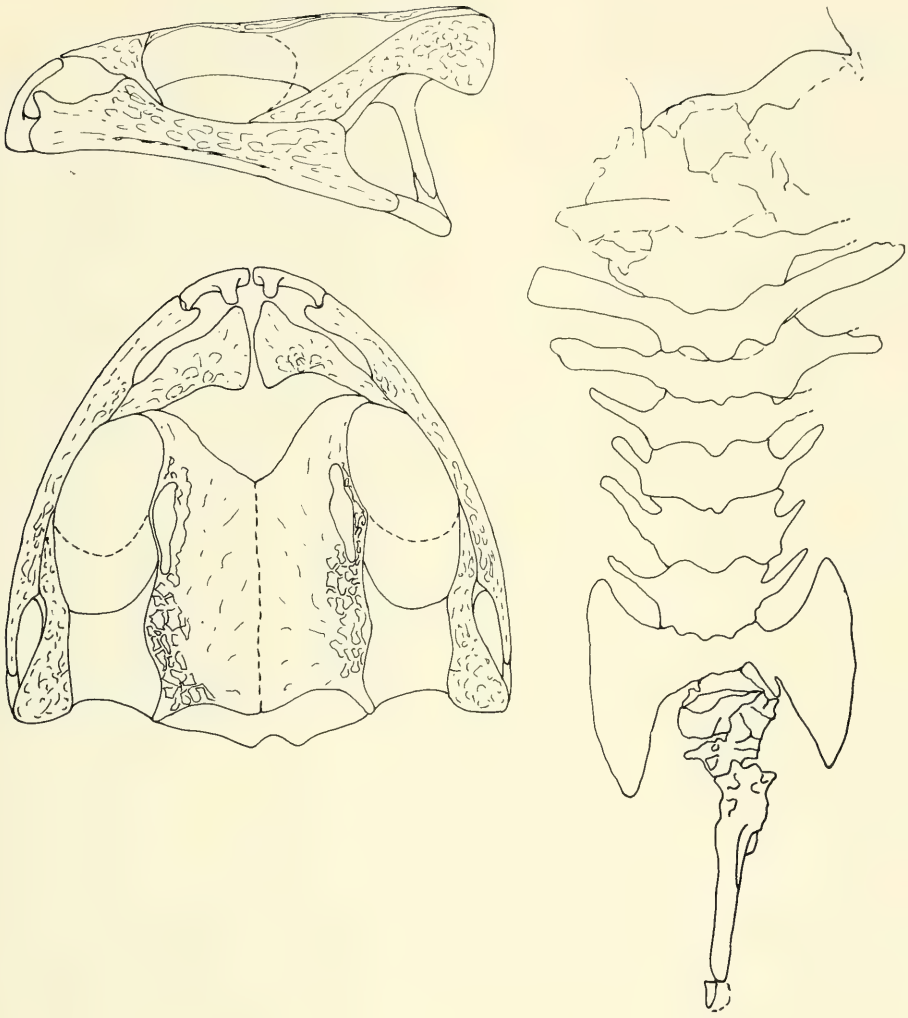

Figure 8. *Eopelobates anthracinus*, type, BM R-4841; left, restoration of dorsal and lateral views of skull; right, camera lucida drawing of vertebral column, posterior skull roof outline shown anteriorly; × 6.

Without the knowledge that the large rodlike anterior process is present in cartilage in *Pelobates cultripes*, the similarities of *Pelobates fuscus* and *Scaphiopus* in ethmoid construction might seem to indicate that the spadefoot genera are closely related through *P. fuscus*, but the latter is not likely to be ancestral to the North American spadefoots, as is discussed further below. *Scaphiopus holbrooki*, the most primitive member of the genus, is intermediate between *P. cultripes* (or *P. syriacus*) and other *Scaphiopus* in this regard; *S. couchi*, *S.* (*Spea*), and *P. fuscus* have independently ossified the anterior process of the ethmoid as far anteriorly as the premaxillae.

It would be of considerable interest to study olfaction within the pelobatines; their nasal capsules indicate some strong adaptive trends not seen in the aquatic *Megophrys* and *Eopelobates*.

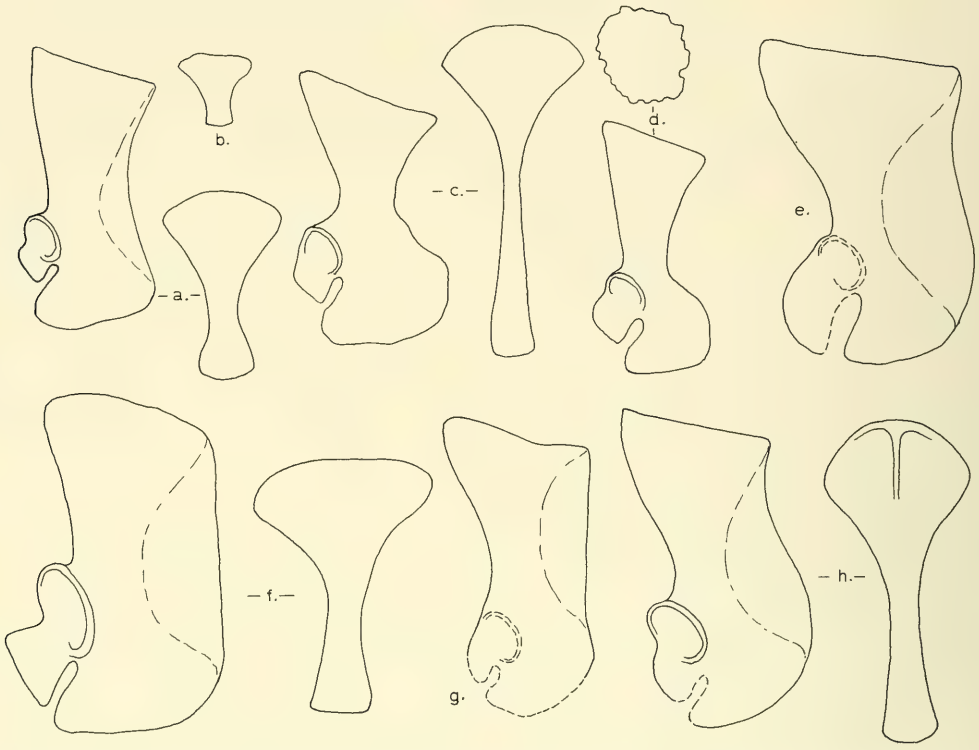

Figure 9. Scapulae and sternal styles of pelobatids. a, *Pelobates cultripes*, UMMZ S-2629; b, *P. syriacus balcanicus*, MCZ 50690, style only; c, *Megophrys monticola*, AM 23964; d, *Scaphiopus couchi*, MCZ 64374; e, *Eopelobates hinschei*, MME 6692, scapula only; f, *E. grandis*, PU 16441; g, *E. anthracinus*, BM R-4841, scapula only; h, *E. bayeri*, CUPI 6.874; a–g, × 3; h, × 4.5.

Chronological Review of Described Eopelobates

CLASS AMPHIBIA
SUPERORDER LISSAMPHIBIA
ORDER SALIENTIA
Family Pelobatidae

Eopelobates anthracinus Parker 1929

Parker's account is good, but better knowledge of other species allows some additional discussion. In the skull, the pattern is approximately as Parker described it, but contrary to the implication of his figure, there is no process of the squamosal leading towards the frontoparietal; this is partly the result of the bone being underlain by the pterygoid and partly the result of crushing in the area. Also, the squamosal is more hatchet-shaped posteriorly than in his figure. The frontoparietal shows prominent, well-defined pits on the lateral edges, and sculpture is more apparent laterally than medially. Because of crushing, the exact shape of the frontoparietal is difficult to determine, but it is about as indicated in Figure 8. There is a groove between the two halves of the frontoparietal that probably indicates a suture, but since all adult *E. bayeri* specimens appear fused, this cannot be certain. There is a complete maxillary arcade; the quadratojugal can be seen clearly on the photograph (Fig. 1), and there is a strong quadratojugal process of the maxilla. The teeth are pedicellate. The bone in the left orbit that

Figure 10. *Eopelobates hinschei*, MME 6692; × 3; see Table 1, 8a.

Table 1
Synonymy of *Eopelobates hinschei*

Eopelobates hinschei (Kuhn)

1. *Halleobatrachus hinschei*, type, MME 1312, Kuhn, 1941, p. 353, pl. I, fig. 1.
2. *Parabufella longipes*, type, (unique specimen, no number?), ibid., p. 358, pl. 4, fig. 5.
3. *Palaeopelobates geiseltalensis*, type, MME 6695, ibid., p. 360, pl. 1, fig. 5.
4. *Archaeopelobates efremovi*, type, (no number), ibid., p. 361, pl. 3, fig. 6.
5. *A. eusculptus*, type, MME 6728, ibid., p. 362, pl. 4, fig. 1.
6. *Amphignathodontoides eocenicus*, type, MME 6744, ibid., p. 364, pl. 6, fig. 1.
7. *Germanobatrachus beurleni*, type, MME 6719, ibid., p. 368, pl. 2, fig. 4.
8. The following specimens referred by Kuhn to the above genera are also referable to *E. hinschei*:
   a. *Palaeopelobates geiseltalensis*, MME 6692, pl. 1, fig. 4.
   b. *P. geiseltalensis*, pl. 2, fig. 5.
   c. *P. geiseltalensis*, MME 6696, pl. 3, fig. 2.
   d. *P. geiseltalensis*, pl. 3, fig. 7.
   e. *cf. Archaeopelobates eusculptus*, pl. 2, fig. 1.
   f. *cf. A. eusculptus*, MME 6762, pl. 4, fig. 3.
   g. ?*A. efremovi*, MME 1572
   h. *Opisthocoelellus weigelti*, pl. 4, fig. 2 (not the holotype).
   i. *O. weigelti*, MME 4995, pl. 5, fig. 2 (not the holotype).

Parker thought was the dentary is actually the prearticular. The anterior tip of the parasphenoid appears to be visible near the anterior end of the left frontoparietal, but the impression is vague. In the postcranial skeleton, imprints of transverse processes on all vertebrae occur on the matrix, contrary to Parker's statement: these are long on the anterior vertebrae but short and anteriorly directed on the posterior ones (Fig. 8) in accord with other species of *Eopelobates*, *Pelobates*, and some *Megophrys*. Again contrary to Parker, the cleithrum is visible on the morphological left side.

Parker remarks (1929, p. 280) that the skull "appears to have been almost identical with that of the recent *Pelobates*." In fact, the skull differs from that of *Pelobates* and *Scaphiopus* and resembles that of other *Eopelobates* in having a flattened or concave skull table and in having approximately subequal orbit and temporal openings. The dermal sculpture is coarse and open, more or less as in the other European *Eopelobates*.

There is an anterior lamina on the scapula (Fig. 9). The urostyle is separate and there were two, perhaps three, postsacral vertebrae, although crushing makes the exact number uncertain (Fig. 8).

The skull restoration of *Eopelobates anthracinus* (Fig. 8) was made from camera lucida tracings of the individual bones; the tracings were then fitted together. Since the bones were all flattened after burial, their somewhat different shape in the restoration results from curvature incorporated into the three dimensional

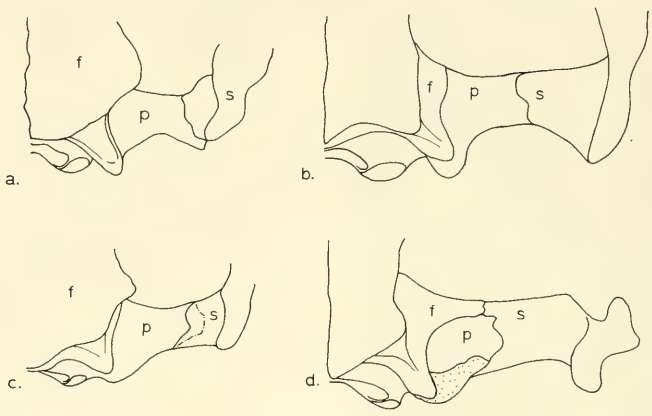

Figure 11. Right posterior half of pelobatid skulls, dorsal view. *a, Scaphiopus h. holbrooki*, MCZ 58003; *b, Eopelobates guthriei*, MCZ 3493; *c, Pelobates fuscus*, MCZ 1012; *d, Megophrys lateralis*, AM 23549; all × 3. f = frontoparietal; p = prootic; s = squamosal; — . — . — . — = margin of prootic covered by squamosal; cartilage stippled.

model. The skull height (especially anteriorly) is the major feature in doubt, but as given it is approximately intermediate between the flattened skulls of *Megophrys* and the domed skulls of *Pelobates* and *Scaphiopus*. The bone outlines do not allow much deviation either way from the outline suggested here. There is a well-defined groove between the frontoparietals, but a distinct suture cannot be seen. The exact shape and placement of the nasals is conjectural, but the arrangement given is consistent with what remains of the bones. The photograph of the specimen (Fig. 1) does not allow confirmation of all bone outlines; this was only made possible by comparing many photographs taken with light coming from different angles and from drawings made at the time of study of the original specimen.

Eopelobates hinschei (Kuhn, 1941)

This species was originally described as *Halleobatrachus hinschei* by Kuhn (1941, p. 353) from the middle Eocene Geiseltal deposits near Halle, Germany. As Špinar (1967, p. 218) correctly pointed out, this species belongs to the Pelobatidae rather than to the Palaeobatrachidae. Much of the other material described by Kuhn also belongs to the genus *Eopelobates*. All the characters of the genus are clearly visible in this series of specimens. The photograph given here (Fig. 10) shows one of the best skulls available. Kuhn gave six generic and seven specific names to this sample, but on the basis of proportions alone, the fossils can easily be related and demonstrated as a growth series (Fig. 25). Hecht (1963, p. 23) has already commented accurately on the reliability of Kuhn's study, but contrary to Hecht, however, Špinar (1967) has shown the presence of palaeobatrachids at Geiseltal.

I think it unlikely that *Eopelobates bayeri* (Špinar, 1952) is conspecific with *E. hinschei*. As Figures 19 and 20 show, the squamosals are different, and there are proportional differences of the nasals. However, the two species are related and both have rather elongated frontoparietals, though that of *E. bayeri* is fused (Fig. 12). Their scapulae are also similar (Fig. 9e, h), as is their ratio of tibiofibula-femur to head-vertebral column length (Fig. 29). Prof. Špinar is presently studying the specimens of *E. hinschei* and *E. bayeri*, and his report will deal with this matter more fully.

Table I lists the synonymy of *Eopelobates hinschei* as I interpret the Geiseltal remains.

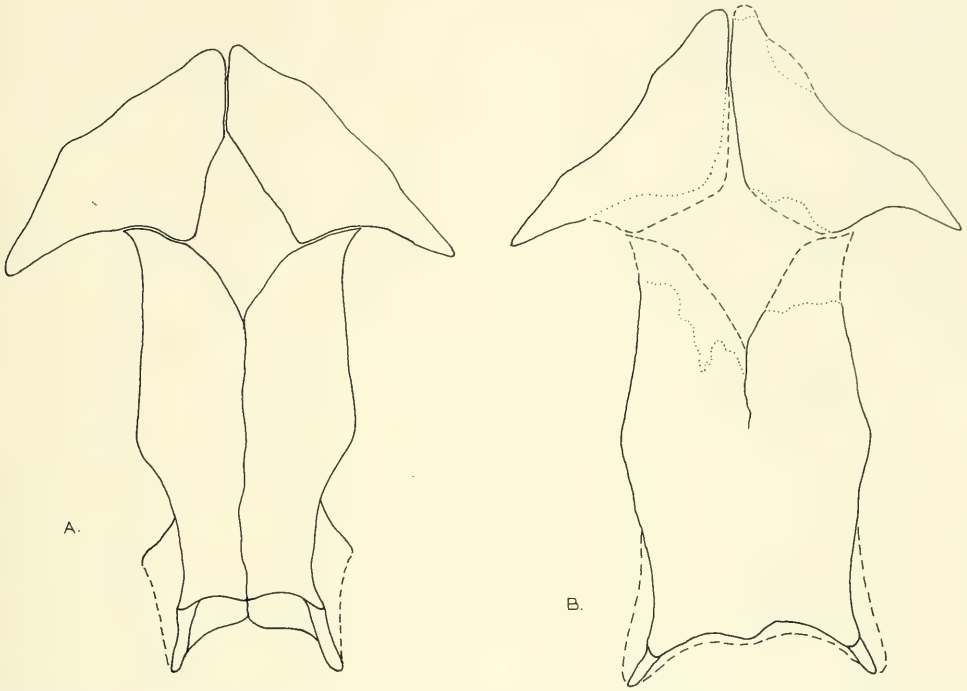

Figure 12. Skull roof of (A) *Eopelobates hinschei*, MME 6692 (8a, Table 1), × 4.5; (B) *E. bayeri*, CUPI 6.874; × 4.8; dashed line = restoration; dotted line = broken bone outline.

Eopelobates bayeri Špinar 1952

As the figure shows, the late Oligocene —middle Miocene Czechoslovakian species *E. bayeri* has all of the characters of the genus noted above (Figs. 2, 12b). Variation may exist with respect to fusion of urostyle and sacrum; in the type specimen of *E. bayeri*, they appear to be separate (perhaps because of poor preservation), but in the new complete specimen are apparently fused. They are separate in *E. bayeri* tadpoles as in tadpoles generally. *E. bayeri* has a somewhat similar squamosal to *E. anthracinus*, but other features, such as frontoparietal shape and ratio of limb to body (Fig. 29), are different. Both species have more sculpture laterally than medially on the frontoparietal, but *E. bayeri* lacks the large pits seen in *E. anthracinus*. The two species seem quite clearly different. The Czechoslovakian material confirms the absence of a spade, and the orientation and shape of the transverse processes is in accord with those of the other specimens of *Eopelobates*, some *Megophrys*, and *Macropelobates*.

Of special interest is the shape of the ethmoid, which is well shown on the new specimen of *Eopelobates bayeri* (*cf.* Figs. 2, 6). It is similar to that of *E. guthriei* n. sp. (see p. 312) but differs from that of *E. grandis*.

The exact contour of the nasals is conjectural. They have been thrust backward over the frontoparietals, and their relations to the latter in the restoration have been determined by triangulation with other skull parts and by comparison with other *Eopelobates* specimens (including the type of *E. bayeri*). On the left side of the restoration (morphological right; the specimen is an imprint), the two parts of the

nasal thrust apart by crushing have been rejoined. Compensation for flattening of the nasals in preservation has been made laterally in the restoration in order to make all restorations comparable.

Eopelobates neudorfensis (Wettstein-Westersheimb, 1955) was based on disarticulated elements derived from a Middle Miocene (Helvetian) fissure filling in southern Czechoslovakia. Most of the diagnostic elements are preserved. The frontoparietal is fused except at the anterior margin and is indistinguishable from that of the new specimen of *Eopelobates bayeri*. The squamosal has a hatchet-shaped tympanic process as in *E. bayeri* and *E. anthracinus* (Fig. 19c). The maxilla has a strong posterior process for the quadratojugal. Urostyle and sacrum are separate. The close association of this species with *E. bayeri* in morphology, time, and geography indicates that it is a synonym of the latter.

Eopelobates grandis Zweifel 1956

A few additions and corrections can be made to Zweifel's excellent account of this early Oligocene North American species (Zweifel, 1956). Although the maxilla and squamosal are in firm contact, there is *no* contact of squamosal and frontoparietal as Zweifel indicated (1956, p. 5). The right squamosal, on which he apparently based this interpretation, has been rotated and displaced up against the frontoparietal. Normal relationships to the frontoparietal are retained by the left squamosal, as confirmed by *Eopelobates anthracinus*, *E. bayeri*, and *E. guthriei* n. sp. (see p. 311). The squamosal shape is more rounded than Zweifel's figure indicates, and is essentially a deeper version of the *E. guthriei* squamosal (*cf.* Figs. 19d and 20d). The frontoparietal differs from that of *E. guthriei* and *E. anthracinus*, but, except for being relatively short, it is in accord with that of other *Eopelobates* (Fig. 13a).

The quadratojugal (identified as stapes by Zweifel) is present and is excavated for a posterior projection of the maxilla as in *Megophrys*. The vomer is now exposed (Fig. 7a) and is like that of *Pelobates* in having a rather expanded anterior wing, an almost transversely-oriented tooth row (rather than a patch), and a dorsal flange clasping the side of the ethmoid as in *P. cultripes*. The ethmoid is more megophryine than in any other *Eopelobates*. It is flattened and dilated anteriorly, and has prominent lateral processes that are deeply notched on their ventral surfaces for the palatines (Fig. 7a). The dorsal surface of the ethmoid is little emarginated. The order of difference from ethmoids of other *Eopelobates* is about the same as between those of the modern species *Megophrys carinensis* and *M. robusta* (Fig. 3). The scapula has a well-developed anterior lamina (Fig. 9f), which has a straight anterior border as in *E. anthracinus*.

The wide posterior extent of the nasal resembles that of *E. guthriei* n. sp. (see Fig. 13) and the pelobatines. This resemblance tends to link the two American species, but I believe it unnecessary to distinguish them generically. Zweifel's reference of this species to *Eopelobates* is undoubtedly correct; it is probably a distinct species because of ethmoid shape, wide frontoparietal, and rounded tympanic process of the squamosal. Hecht (1963, p. 23) has suggested that this animal is a distinct genus, but it differs no more from other *Eopelobates* than the Recent *Megophrys carinensis* differs from *M. lateralis*, for instance.

Eopelobates sp.

Hecht (1959, p. 131) described a megophryine sacrum from the middle Eocene Tabernacle Butte local fauna of Wyoming and correctly noted a close resemblance to *Eopelobates grandis* Zweifel. It is reasonable to refer the Tabernacle Butte specimen (AMNH 3832) to *Eopelobates* without specific designation.

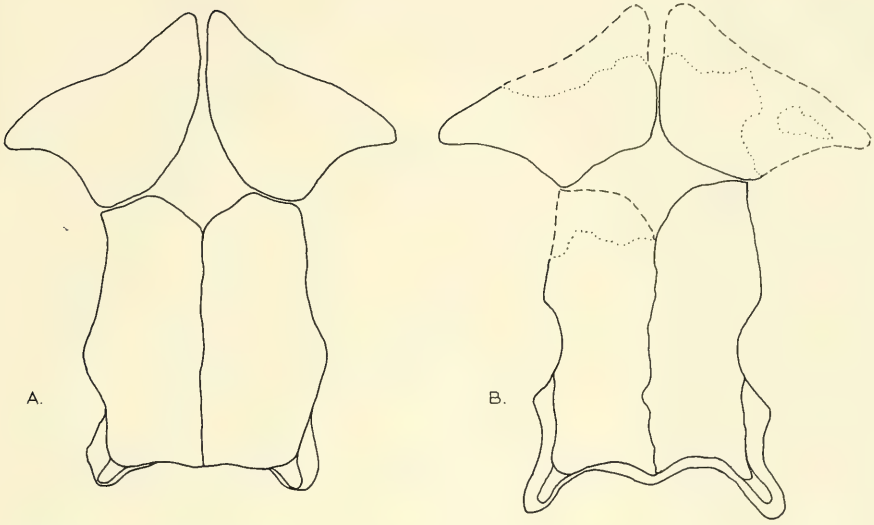

Figure 13. Skull roof of (A) *Eopelobates grandis*, PU 16441, × 1.8; (B) *E. guthriei*, MCZ 3493, × 3. Dashed line = restoration; dotted line = broken bone outline.

Młynarski referred to *Eopelobates* sp. material from the Pliocene of Poland. The specimens consist only of sacra having separate urostyles. Other fused sacra and urostyles and characteristic skull elements he referred to *Pelobates cf. fuscus*. Since, however, *Eopelobates* is otherwise unknown later than middle Miocene, and since *Pelobates cultripes* often has partially or completely separated urostyles, it seems unlikely that *Eopelobates* is represented in the Polish material, at least in the absence of characteristic skull elements. These elements may be referable to *Miopelobates* (see below). Since the salamander *Andrias* is now known to occur in the European Pliocene (Westphal, 1967) there is no apparent reason why *Eopelobates* might not also have persisted, but at present there is insufficient reason to confirm its extension beyond the middle Miocene.

Description of New Material of Eopelobates

Eopelobates guthriei, n. sp.

Type: MCZ 3493, nearly complete skull and associated fragmentary scapula.

Diagnosis: Differs from other species of *Eopelobates* in having a narrow tympanic process of the squamosal combined with a triple emargination of the frontoparietal margins and a relatively short skull.

Etymology: Patronym for Dr. Daniel Guthrie, who collected the unique specimen in 1962.

Locality: NE 1/4, SE 1/4, Sect. 16, T 39 N, R 90 W, Fremont County, Wyoming.

Horizon: Upper part of the Lysite member, Wind River Formation.

Age: Early Eocene (Lysitean, late Sparnacian equivalent).

Preservation: Only the skull, portions of the prearticular region of the jaws, and an associated fragment of left scapula are present (Fig. 14). The slightly crushed skull is well preserved on the right side, but on the left the temporal region is missing. The premaxillae, the anterior portions of the nasals, and the anterior part of both maxillae are missing.

Although the skull is slightly flattened, distortion is limited for the most part to the peripheral tooth-bearing and temporal bones. The ventral borders of the maxillae

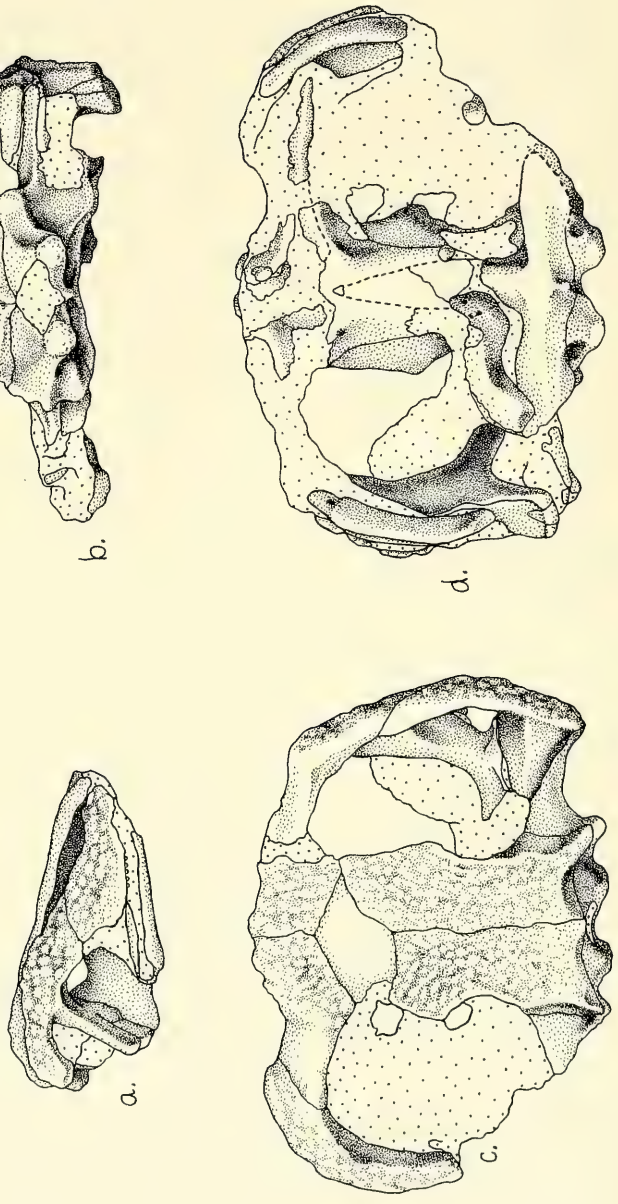

Figure 14. *Eopelobates guthriei*, n. sp.; holotype skull, MCZ 3493; *a*, right lateral, *b*,occipital, *c*, dorsal, and *d*, ventral views; early Eocene, Wyoming; × 2; coarse stipple = matrix.

are warped laterally, a condition especially true of the left maxilla, whose lateral aspect now faces almost dorsally. Ventrally, the left palatine has been pushed dorsally away from the ethmoid, but it seems to have retained its natural relationship to the latter.

Description: The skull indicates a rather broad-headed animal with subequal dorsal temporal excavations and orbits, separated by postorbital processes. The dorsal skull region is flattened and concave medially and bounded by weak crests. The skull as a whole is covered with a well-developed dermal sculpture.

Posteriorly the nasals meet on the midline, diverge at their posterior borders to expose the ethmoid, barely meet the frontoparietals, and extend laterally to meet the maxillae. The nasals are weakly crested in the area continuous with the lateral borders or the frontoparietals, and slope toward the midline between these crests. The nasals are sculptured on their entire preserved surface.

Located between the frontoparietals and the nasals is a smooth, somewhat diamond-shaped portion of the ethmoid, which is the center of a depression bounded anteriorly by the nasal crests mentioned above and posteriorly by the lateral borders of the frontoparietals. The depression extends to the posterior border of the skull.

The paired frontoparietals are subrectangular in shape and prominently sculptured. The postorbital processes are situated anteriorly about two-thirds the frontoparietal length from the apex of the foramen magnum. The anterior tip of the left frontoparietal is missing, increasing the apparent depth of the ethmoid depression. The anterior tip of the right frontoparietal touches the nasal at its lateral border. The undistorted occiput, the lateral crests of the frontoparietals, and the symmetry of the cranial roof indicate that the midline depression of the frontoparietal, ethmoid, and nasals is natural. The postorbital processes are the widest points on the frontoparietals except for the posterior tips, which extend onto the paired projections of the paroccipital processes on the occiput dorsal to the condyles. Posteriorly the frontoparietal reaches the apex of the foramen magnum, from which point lambdoidal crests form concave curves, extending towards the paired projections noted above.

In occipital view the median skull roof is depressed; the highest points are on its lateral borders. The occipital surface of the skull is well preserved and relatively little distorted; there is little breakage except for the missing left temporal region. The most prominent bones are the otoccipitals, which meet above and below the triangular foramen magnum. The large circular foramina for the ninth and tenth cranial nerves are recessed at the base of the prominent hemispherical occipital condyles. Lateral to these foramina, the otoccipital forms the posterior border of the fenestra ovalis, forming a prominent rounded process underlain by the parasphenoid. Laterally the otoccipital forms a prominent knobbed paroccipital process, which is capped by the frontoparietal. The stapes is forked proximally and is closely appressed to the ventral surface of the lateral extension of the otoccipital. The fenestra ovalis is open ventral to the proximal end of the stapes and dorsal to the rounded process of the otoccipital mentioned above; a large opercular space is present as in recent spadefoots, and since the very delicate stapes is preserved in place, a calcified operculum was probably absent.

The right squamosal has been displaced dorsally at its posterior articulation with the otoccipital; in fact it has pivoted somewhat (along with pterygoid and maxilla) on the lateral tip of the otoccipital, so that the greatest dorsal displacement is at the medial end of the squamosal, and the descending (quadrate) process of the squamosal has been rotated mediad, carrying with it the remains of the lower jaw. The quadrate is represented by a small sliver

clasped between squamosal and pterygoid. The posterior end of the lower jaw is missing, as are the tip of the quadrate and the posterior border of the maxilla; apparently the quadratojugal and posterior process of maxilla (if present) were broken off in the dislocation of the temporal region.

In the ventral view, the posterior portion of the parasphenoid is well preserved, but the cultriform process is faulted by the right scapula and then terminates by breakage at the ethmoid border. The parasphenoid extends anteriorly from the border of the foramen magnum to the posterior border of the ethmoid. The lateral arms of the parasphenoid form the floor of the fenestra ovalis region. Prominent nuchal, pterygoid, and retractor bulbi muscle scars, set off a trapezoidal, flattened area midway between the lateral arms of the parasphenoid.

The otoccipitals extend posteriorly somewhat beyond the posterior borders of the parasphenoid, completing the fenestra ovalis region ventrally.

There is a large opening in the posterior braincase region, bounded anteriorly by ethmoid, ventrally by parasphenoid, posteriorly by otoccipital, and dorsally by frontoparietal. The major cranial nerves emerged through this opening, but only the prootic foramen has any individuality. It is a narrow suboval notch, open anteriorly.

The ethmoid is broadly exposed between the parasphenoid and the vomers, and ventral processes of the frontoparietals clasp it laterodorsally. It sends broad, crested processes laterally toward the maxillary arcades, and posterodorsal to each of these open the foramina for the anterior (orbital) extensions of branches of the occipital arteries. Anterior to each lateral ethmoid process is a depression, from which bone is missing as a result of erosion and breakage. Anterior to these depressions, the curved choanal borders of the vomers are still preserved in natural position. A raised area over the left anterior part of the ethmoid probably represents the left vomerine tooth plate. The other parts of the vomers are not preserved. Laterally, an irregular, broken bar of bone seen on the left side probably represents the palatine.

The pterygoid is present as a complete bone only on the right side, and is strongly curved, bending broadly toward the quadrate region on the one hand, and toward the otoccipital and maxilla on the other.

In lateral view the relationships of the maxilla, squamosal, quadrate, pterygoid, and prearticular are undistorted on the right side. On the left side, only the middle part of the maxilla is present; the temporal region and premaxilla are missing.

The maxillae bear pedicellate teeth and are heavily sculptured in a pattern similar to that of the frontoparietals. On the right side, the posterodorsal corner of the maxilla meets the squamosal in a broad horizontal suture.

TABLE 2

MEASUREMENTS OF *EOPELOBATES GUTHRIEI*

The following measurements (in mm) are relatively unaffected by crushing or distortion:		
1.	posterior median height of the skull from the most dorsal point on the frontoparietals to the most ventral point on the midline of the parasphenoid	4.9
2.	height of foramen magnum	2.0
3.	width of foramen magnum	4.0
4.	maximum width across the paroccipital processes	11.1
5.	maximum width across occipital condyles	6.2
6.	maximum length of stapes as preserved	4.7
7.	maximum length of frontoparietal from apex of foramen magnum to anterolateral tip	12.0
8.	length from apex of foramen magnum to postorbital process	8.3
9.	maximum anteroposterior length of right squamosal	11.2
10.	length of posterior projection of squamosal behind anterior margin of tympanic cavity	5.0
11.	maximum width across postorbital processes of frontoparietals	9.0
12.	maximum height of posterior process of squamosal	2.0

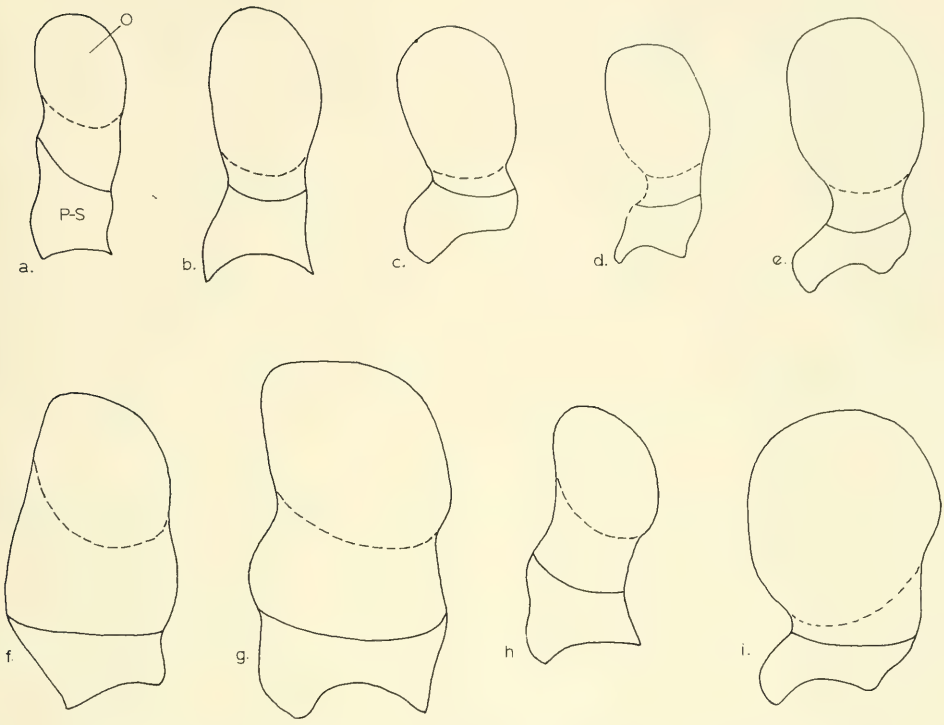

Figure 15. Orbitotemporal opening relationships in pelobatids; all are of right side, anterior towards the top. *a, Eopelobates anthracinus*, BM R-4841; *b, E. grandis*, PU 16441; *c, Pelobates fuscus*, MCZ 1012; *d, Scaphiopus skinneri*, FAM 42920; *e, S. holbrooki*, MCZ 58003; *f, Megophrys carinensis*, AM 23965; *g, E. hinschei*, MME 6692; *h, E. guthriei*, MCZ 3493; *i, S. couchi*, AM 14478. Not to same scale; O = orbit; P–S = prootic and squamosal roof of ear region; dashed line = posterior border of orbit in all, and restored portion of frontoparietal in *d*.

The T-shaped squamosal is well preserved on the right, and, like the maxilla, is sculptured on the crossbar of the T. Anteriorly the bone is much broader than it is posteriorly. The posterior process of the squamosal curves posteriorly over the tympanic cavity, expands slightly at its posterior border, and forms an acute angle with the descending process of the squamosal. The latter process is flattened anteroposteriorly and has a sharp crest separating the tympanic cavity from the lower temporal excavation. The descending process is closely applied to the posterolateral border of the pterygoid, and is separated from it ventrally by the sliver of quadrate noted in the description of the occipital view. The ventral portion of the quadrate is lost, as is the articular. Pieces of the prearticulars indicate the position of the lower jaws, and lie in their natural positions ventromedial to the maxillae.

The crushed and fragmentary left scapula has been rotated 180° and now lies on the right side. Its posterior border is broken and little, if any anterior lamina appears to have been present.

Discussion: Because of the possession of a concave skull roof, approximately subequal orbital and temporal openings, and the distinctive shape of squamosal and ethmoid (Figs. 14, 13b, 19, and 20), reference of this specimen to *Eopelobates* seems clear.

In the proportions of nasals and frontoparietals, *E. guthriei* shows the relatively short skull characteristic of pelobatines and *E. grandis*, whereas the European

species, except for *E. anthracinus,* are more elongated and megophryine in these characters. *E. anthracinus* also shows the triple frontoparietal emargination of *E. guthriei,* but in squamosal shape there is close agreement between *E. guthriei* and the middle Eocene *E. hinschei* from the Geiseltal. In both of the latter, the anterior maxillary process of the squamosal is more expanded than the tympanic process, which is narrow and forms a wide, laterally visible roof to this part of the tympanic cavity. This roof lacks dermal sculpture (Fig. 20b, d, R). In dorsal view, *E. guthriei* resembles *Scaphiopus* and *E. grandis* in the excavation of the posterior border of the otoccipital and squamosal (Fig. 15).

The ethmoid of *E. guthriei* is incomplete and poorly preserved anteriorly but seems to resemble that of *E. bayeri* and (so far as can be seen in the crushed material) *E. hinschei;* it is relatively shorter as a result of the less elongate skull of the American form. The vomer has a broad, flat process on the posterior border of the choana as in *Leptobrachium hasselti,* the most primitive megophryine (Inger, 1966, p. 21) rather than a short, pointed process as in *Megophrys. E. grandis* has a similar process to *E. guthriei,* but it is relatively smaller and closer to the *Megophrys* condition.

The occiput of *E. guthriei* is quite pelobatine in its well-ossified paroccipital processes and tubera, its general proportions and relatively simple stapes. Unfortunately, the occiput is not known in any other specimen of *Eopelobates.*

Comparison of Figures 12, 13, and 17–23 shows that, in combination, squamosal and frontoparietal shape distinguish the modern pelobatid species. Since the specific status of the latter is based on many other criteria not available in fossils, these characters can be confidently applied to fossil samples. Either character separately may be useful, but wherever possible the two should be used together.

By this criterion the separate species

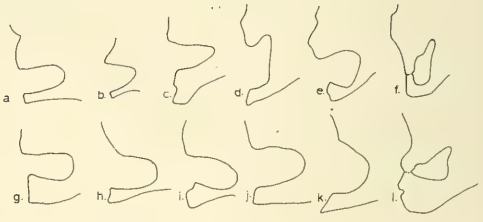

Figure 16. Anterior parts of left prootic bones showing prootic foramina. *a, Megophrys carinensis,* AM 23965; *b, M. monticola,* AM 23964; *c, Eopelobates guthriei,* MCZ 3493; *d, Pelobates fuscus,* MCZ 1012; *e,* the same, MCZ 1353; *f,* the same, right side (reversed); *g, Scaphiopus h. holbrooki,* MCZ 58003; *h, S. skinneri,* FAM 42920; *i, S. h. hurteri,* AM 44244; *j, S. couchi,* AM 57642; *k, S. couchi,* AM 14478; *l, S. intermontanus,* AM 16916. *a–b,* × 2; *c–l,* × 4.

status of *E. guthriei* and the Gieseltal *E. hinschei* is shown by their different frontoparietal proportions. Their squamosals are very similar and show Eocene transatlantic similarities, a phenomenon already observed in many fossil mammals and lizards. Yet there are minor proportional differences between the squamosals of the two Eocene species that are of the order of magnitude seen in modern species such as *Scaphiopus holbrooki* and *S. couchi.*

The frontoparietals of *Eopelobates guthriei,* however, are relatively shorter than in either *E. hinschei* or *E. bayeri,* and are very similar to those of *E. grandis* and *E. anthracinus* (*cf.* Figs. 8, 12, 13). The general proportions of the posterior end of the skull are more as in megophryines than as in pelobatines (Fig. 11); the posterior border of the prootic part of the otoccipital, however, is expanded posteriorly as in *Scaphiopus* (and to a lesser degree in *Megophrys*) but not as in *Pelobates,* in which the tip of the prootic is narrow as in *Macropelobates* (Fig. 11). Unfortunately, this condition is not known in other *Eopelobates.* The prootic foramen of *E. guthriei* (Fig. 16) resembles that of *Megophrys carinensis* and most *Scaphiopus* (*Scaphiopus*) in its rather elongate, simple, and unrestricted opening; there is no approach to the restricted or closed opening seen in *Pelobates* and *S.* (*Spea*).

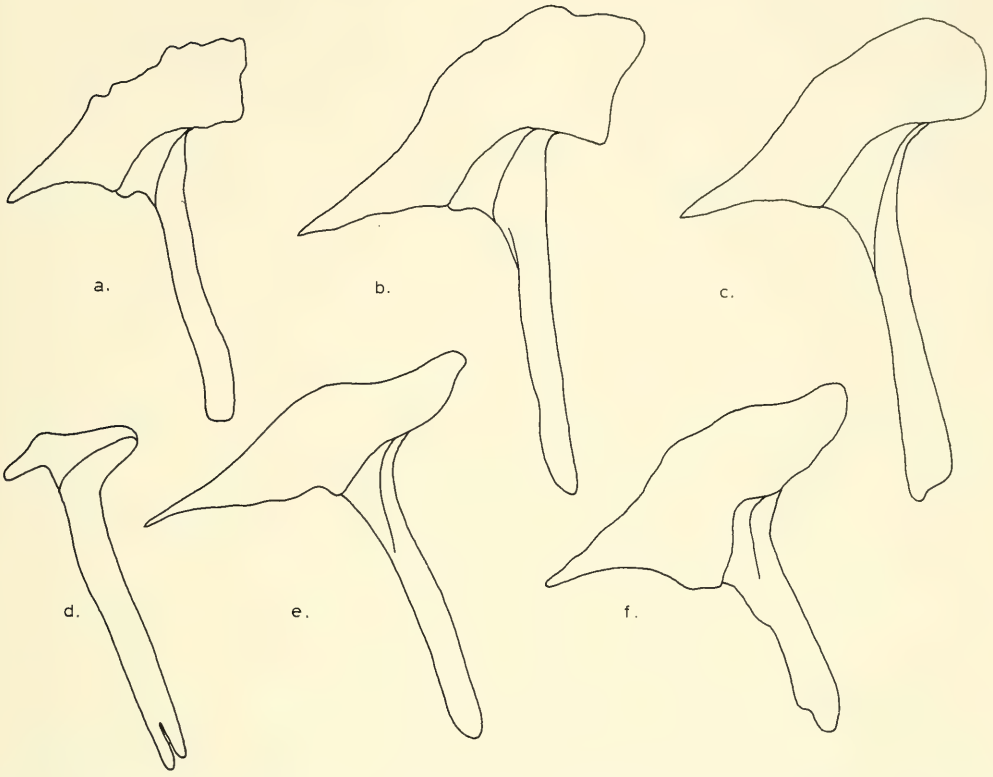

Figure 17. Left squamosals of pelobatids. *a, Scaphiopus couchi*, AM 56284; *b*, the same, AM 57641; *c*, the same, AM 14478; *d, S. intermontanus*, AM 16916; *e, S. holbrooki hurteri*, AM 44244; *f, S. h. holbrooki*, MCZ 58003; all × 6.

?*Eopelobates* sp.

In 1964, I described disarticulated and questionably pelobatid remains from the late Cretaceous Lance Formation of Wyoming. These elements included humeri, ilia, a urostyle, and a maxilla. The ilia (Estes, 1964, fig. 31c) closely resemble those of most pelobatids and the superior acetabular expansion is relatively small as in *Pelobates cultripes*, *Macropelobates*, some *Eopelobates*, and the discoglossids. The urostyle is megophryine in possessing a single articular cotyle and transverse processes; discoglossid and ascaphid urostyles also have the latter but have a double condyle as well.

The squamosal cited as hylid-like (Estes, 1964, fig. 31a-b) closely resembles that of *Eopelobates guthriei* and *E. hinschei* and is probably pelobatid rather than hylid. In 1964, I recognized resemblances of this squamosal to those of pelobatids (p. 60), but lacking knowledge of Eocene *Eopelobates*, I was reluctant to refer a squamosal of such unusual shape to the Pelobatidae. The maxilla (Estes, 1964, fig. 31d-e) lacks sculpture and may not be referable to the pelobatids. A fragment of a maxilla that has sculpture like that of the squamosal is now known (AMNH 8133, V5620, Lance Formation, Wyoming). The nasal questionably referred to the Hylidae (Estes, 1964, p. 60) may also be pelobatid on the basis of sculpture similarity to the other specimens.

It is possible that the Lance Formation specimens may be an early record of either *Eopelobates* or of a related pelobatid per-

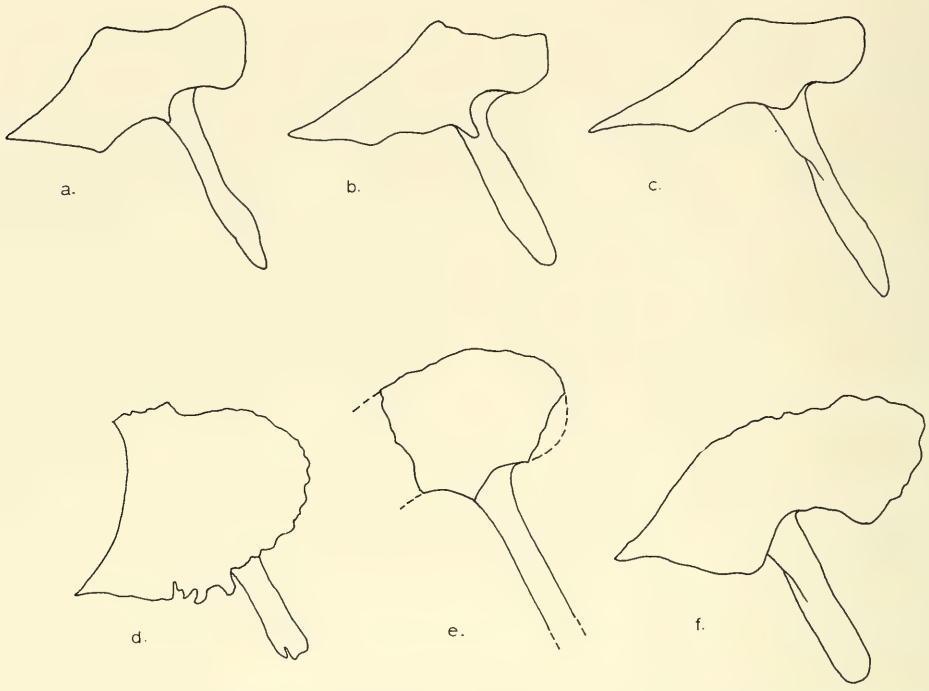

Figure 18. Left squamosals of pelobatids. *a, Pelobates fuscus,* MCZ 1353; *b,* the same, MCZ 1013; *c,* the same, MCZ 1012; *d, P. cultripes,* UMMZ S-2630; *e, Macropelobates osborni,* AM 6252; *f, Scaphiopus skinneri,* FAM 42920. Dashed line = restoration; *a–c,* × 6; *d–f,* × 3.

haps nearer to the discoglossids. Unfortunately, without articulated or at least more extensive material the reference must remain tentative. New material from the Lance Formation and from other late Cretaceous localities has made the association of the remains somewhat more assured now than in 1964. Several discoglossids are present in these localities (Estes, 1969) and are represented by well-preserved and distinctive skeletal elements different from those considered here.

The Relationships of Eopelobates

In his original discussion, Parker (1929, p. 280) suggested that *Eopelobates anthracinus* was a late representative of Noble's (1924, p. 9) "first stage" of pelobatid evolution, one in which ribs, an acromion, reduction of pubis, and expansion of sacral diapophyses were found. Parker also noted a close similarity in the proportions of *E. anthracinus* to those of *Macropelobates.* The latter genus exemplified Noble's "second stage" of pelobatid development by development of prehallux, dermal skull casque, and further expansion of the sacral diapophyses. In 1952, Špinar made more explicit the relationship of *Eopelobates* to *Megophrys* in his discussion of a second species of *Eopelobates.* Zweifel (1956), in describing a third species, *E. grandis,* suggested that *Eopelobates* might be included as a subgenus of *Megophrys,* but that such a course would involve "investigation of other units within *Megophrys* probably worthy of subgeneric rank." The description here of a new Eocene species of *Eopelobates,* the recognition of the excellent series of *Eopelobates* specimens (here referred to as *E. hinschei*) from the Geiseltal middle Eocene, and the new

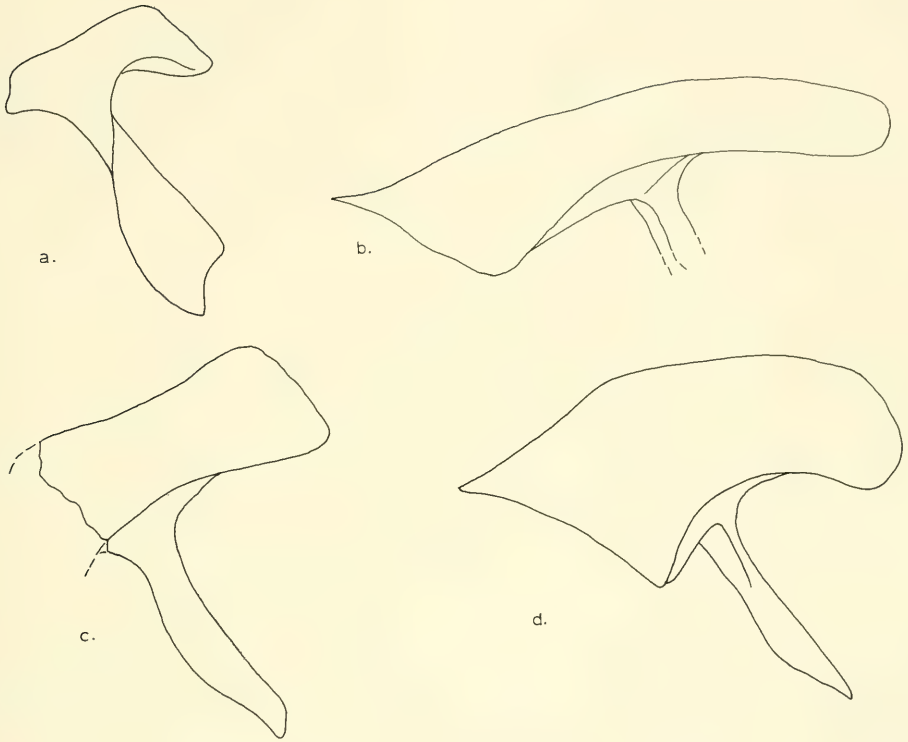

Figure 19. Left squamosals of pelobatids. *a*, *Megophrys lateralis*, AM 23549; *b*, ?*Eopelobates* sp., UCMP 44707; *c*, *E. "neudorfensis"* (= *bayeri*); *d*, *E. grandis*, PU 16441. Dashed line = restoration; *a–b*, × 6; *c*, × 10; *d*, × 3.

specimen of *E. bayeri* make it possible now to take a closer look at the relationships of *Eopelobates*. Redefinition of *Macropelobates* has also been necessary, and this will be discussed below.

Eopelobates was a relatively widespread and common early and middle Cenozoic frog first known with certainty from early Eocene of North America and middle Eocene of Europe. These two forms, *E. guthriei* and *E. hinschei*, respectively, show relationship to each other in their squamosal shape, although *E. hinschei* has already developed the long skull table seen later in *E. bayeri*. The relationship between the two Eocene forms is probably real, however, and demonstrates another similarity in early and middle Eocene continental transatlantic vertebrate faunas (Simpson, 1947). This similarity first appears in the late Paleocene mammalian and lower vertebrate faunas (Russell, 1964; Estes, Hecht, and Hoffstetter, 1966). Yet the time difference and the differentiation into long and short-headed forms indicate that the intercontinental similarity is not so specific as to imply direct connection.

It is possible, as noted above, that *Eopelobates* (or an ancestor) was already present in the late Cretaceous of North America. Relevant material is very fragmentary, however, and the record must be used with care.

Eopelobates does not recur in Europe until the middle Oligocene of Germany, when *E. anthracinus* indicates the presence of the short-headed lineage. The long-headed line begun by *E. hinschei* in the Eocene leads directly to the late Oligocene

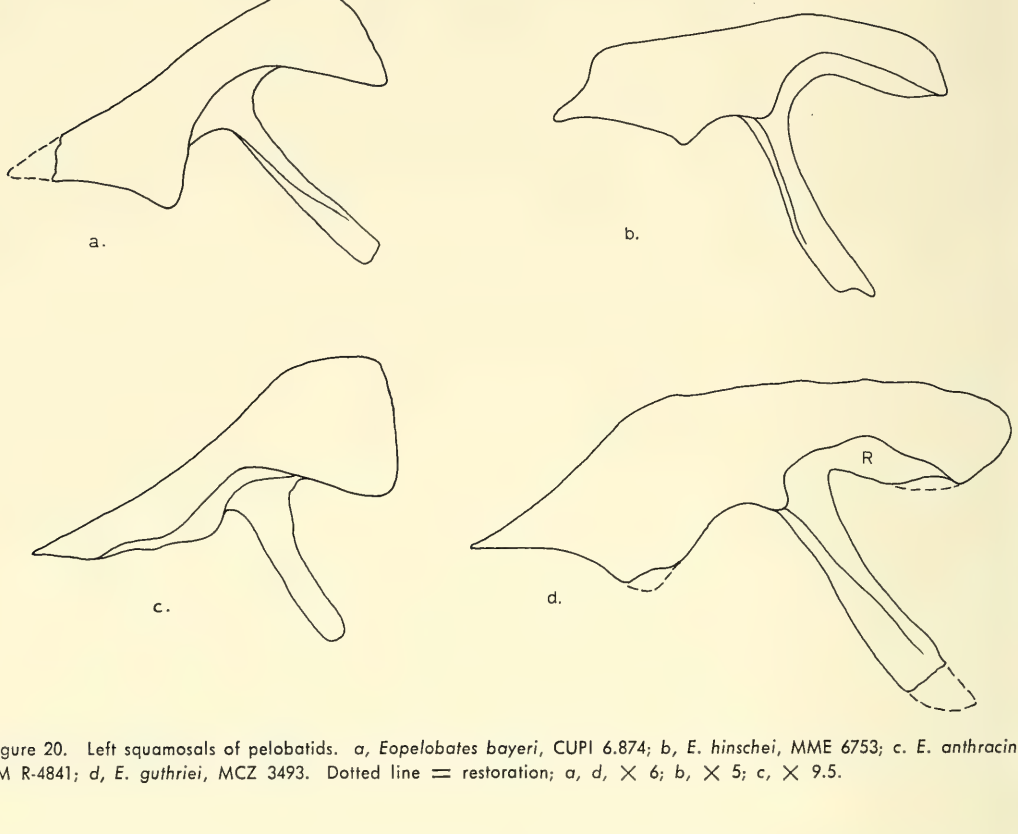

Figure 20. Left squamosals of pelobatids. *a, Eopelobates bayeri*, CUPI 6.874; *b, E. hinschei*, MME 6753; *c. E. anthracinus*, BM R-4841; *d, E. guthriei*, MCZ 3493. Dotted line = restoration; *a, d,* × 6; *b,* × 5; *c,* × 9.5.

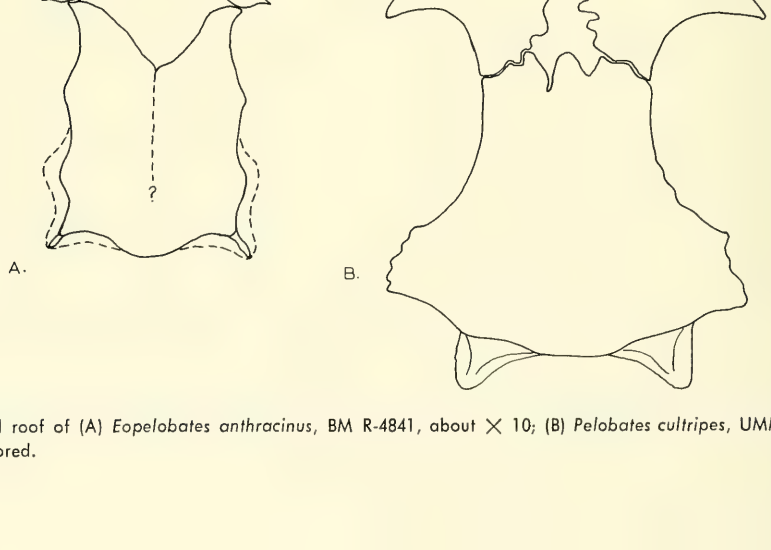

Figure 21. Skull roof of (A) *Eopelobates anthracinus*, BM R-4841, about × 10; (B) *Pelobates cultripes*, UMMZ S-2631, × 3; dashed line restored.

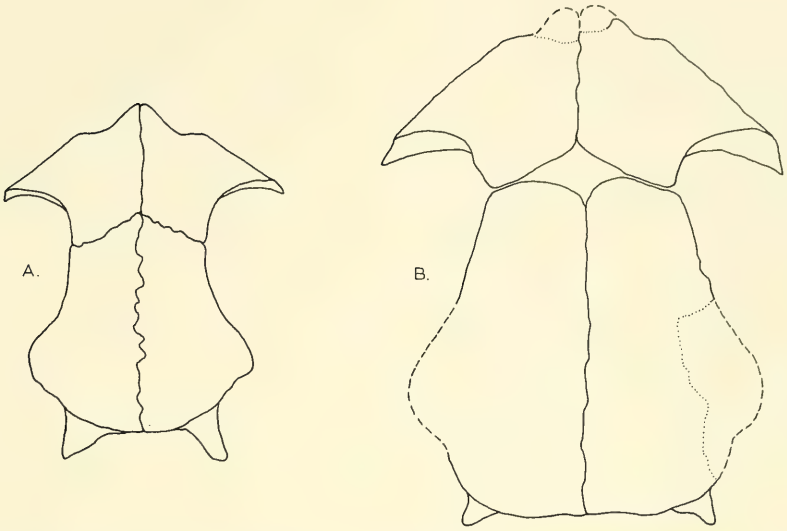

Figure 22. Skull roof of (A) *Scaphiopus h. holbrooki*, MCZ 58003; (B) *S. skinneri*, FAM 42920; both × 3. Dashed line = restoration; dotted line = broken bone outline.

(or early Miocene) and middle Miocene *E. bayeri* from Czechoslovakia. In North America, *E. grandis* continues the short-headed line into the early Oligocene but then apparently becomes extinct.

Eopelobates is characterized by a number of features listed at the beginning of this paper, the most distinctive being generally long-limbed proportions, absence of dermal head casque fused to the skull. The body proportions differ from those of most megophryines in having a greater relative elongation of the vertebral column and urostyle as well as a lengthening of limb segments, especially the tibiofibula, which is significantly longer than the femur. In

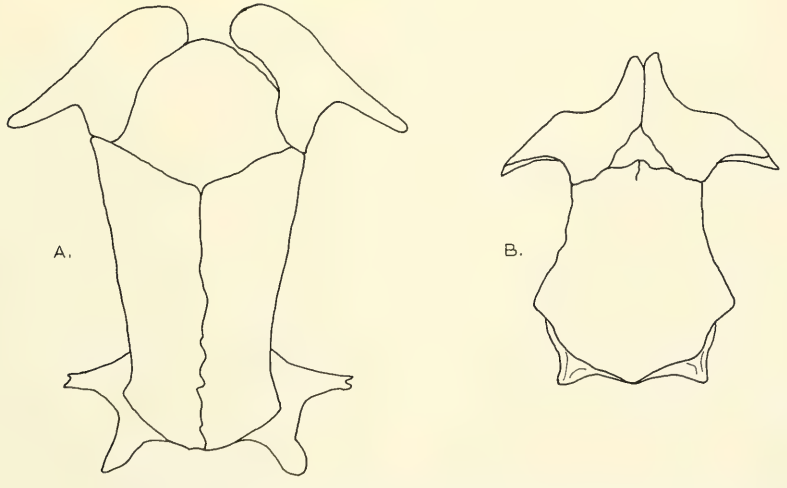

Figure 23. Skull roof of (A) *Megophrys lateralis*, AM 23549; (B) *Pelobates fuscus*, MCZ 1012; both × 3.

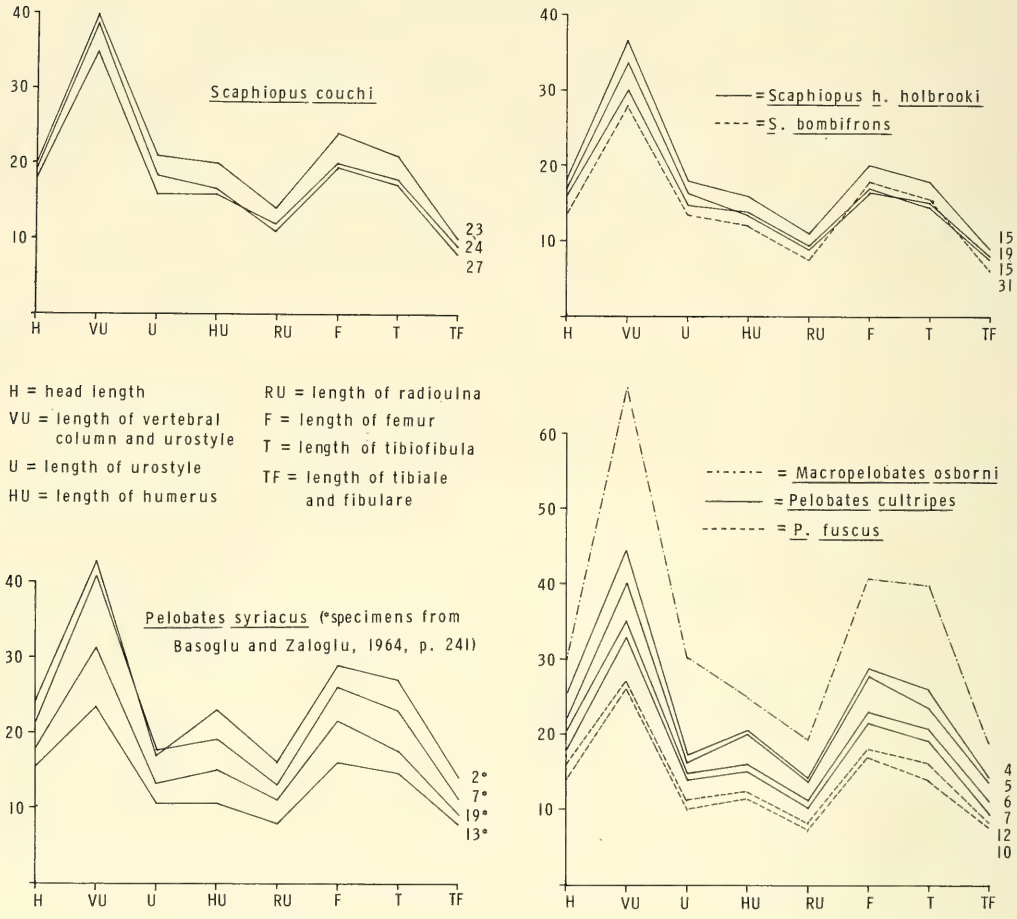

Figure 24. Body proportions of pelobatids. Measurements in millimeters.

pelobatines, the tibiofibula is always a spade, and possession of a well-developed shorter than the femur.

With increasing body size, all pelobatids show allometry in the vertebral column and hind limbs relative to other parts of the skeleton (Figs. 24–25), and the allometric pattern is distinctive for the individual groups. Within the megophryines, the primitive *Leptobrachium* (see Inger, 1966) has head and vertebral proportions as in *Pelobates* rather than as in *Megophrys;* some similarity to *Eopelobates* (especially *E. anthracinus*) occurs as well. So far as my few specimens indicate, the mainland species *M. aceras* shows an *Eopelobates*-like elongation of the tibiofibula whereas the East Indian *M. monticola* and *Leptobrachium hasselti* have a subequal femur and tibiofibula. The Burmese specimen of *M. carinensis* has a tibiofibula slightly shorter than the femur, a proportion reminiscent of pelobatines. Two groups within *Megophrys* seem distinguishable on the basis of the few species and specimens available to me: the one group having relatively short, anteriorly-directed posterior transverse processes, fused urostyles, and body proportions like those of *Eopelobates hinschei;* the other

Figure 25. Body proportions of pelobatids and discoglossids. Measurements in millimeters.

group having loose urostyles, elongated, more perpendicular posterior transverse processes, and limb proportions closer to those of the pelobatines. The latter group is less *Eopelobates*-like in the last two features.

Leptobrachium is primitive in having short, anteriorly-directed posterior transverse processes as in *Eopelobates* and (to lesser degree) as in pelobatines. The first group of *Megophrys* noted above is more like *Leptobrachium* in this regard; the second and more terrestrial group is distant from the latter and approaches the terrestrial pelobatines in limb proportions.

Zweifel (1956, p. 13) emphasized the relationship of *Eopelobates* and *Megophrys* first noted by Špinar (1952, p. 487).

The characters used by Zweifel require some qualification and are discussed *seriatim*:

(1) ". . . only the complete postorbital arch will distinguish [*Eopelobates*] from [*Megophrys*]." As noted above, a squamoso-frontoparietal arch does not exist in *Eopelobates*. In pelobatines this arch is present only in *Pelobates cultripes* (lacking in small individuals), and in most *P. syriacus* (Başoğlu and Zaloğlu, 1964, p. 239). This condition is discussed more fully in the section on anatomical features at the beginning of this paper.

(2) Long transverse processes of the second, third, and fourth vertebrae are present in *Eopelobates* and in most *Megophrys*. In *Eopelobates* their breadth is equivalent to the length of from five to seven vertebrae; the greater the number, the larger the specimen. In *Megophrys* the range is from four to seven vertebrae, again increasing with size. In *Pelobates* this breadth covers only from four to five vertebrae; even the large *P. cultripes* and *Macropelobates* do not exceed this figure. In *Scaphiopus* the range is from four to six vertebrae, and the entire range is encompassed by the *S. couchi* specimens in my sample. This character is therefore not entirely clearcut, but *Eopelobates* and *Megophrys* show the greatest general similarity.

(3) The greatly expanded sacral diapophyses common to *Eopelobates* and some *Megophrys* can be duplicated in *Pelobates cultripes*. The length of the diapophyses in the latter is equivalent to the length of about four or five presacral vertebrae, in *Eopelobates* the range is about four to seven vertebrae, and in no *Megophrys* available to me does it exceed 3.5 vertebrae.

(4) The shape of the bony sternal style is similar and the bone is elongated in both *Eopelobates* and *Megophrys*. However, in *Pelobates cultripes* the shape is close to that of *E. bayeri* and *E. grandis* and is relatively wider throughout its length in these three species than in *Megophrys* of equal size (Fig. 9).

(5) The free urostyle with transverse processes is similar in some *Megophrys* and some *Eopelobates*, and fusion is variable in both genera. The urostyle of *Pelobates cultripes* is also suturally separate, although partial fusion may have taken place internally. As has been pointed out by many authors (most recently Kluge, 1966), this character is of little value as presently understood. However, some of the intraspecific variation noted in *Megophrys* by various authors was the result of incorrect identification; this character may deserve more careful study.

(6) The great posterior extent of the ischium is similar in both *Megophrys* and *Eopelobates*. Some approach to this condition may be found in *Macropelobates* but the latter more closely resembles *Pelobates cultripes* in this regard (Fig. 26). In this respect the megophryine resemblance is more clear cut.

Thus only 1 and 6 are clear cut resemblances (but to different subfamilies), 2 is perhaps megophryine, 3 and 4 resemble both subfamilies, and 5 is inconclusive. The following characters further emphasize the mosaic of megophryine and pelobatine characters of *Eopelobates*. The *Eopelobates* ethmoid resembles that of the megophryines; in the prootic foramen (known only in *E. guthriei*) and orbitotemporal opening there are resemblances to both subfamilies; in body proportions the variation in pelobatines and *Eopelobates* is encompassed by that found in *Megophrys*. *Eopelobates* (except *E. guthriei*) has a broad, thin, anterior lamina on the scapula that is well developed even in the small *E. anthracinus*. Among pelobatines, only *Pelobates* has such a structure, although it is less well developed.

Intrageneric Classification

From the above it is clear that *Eopelobates* is not a subgenus of *Megophrys* as Zweifel (1956, p. 13) suggested. Although

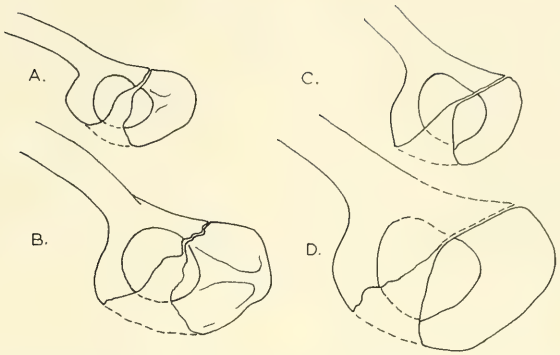

Figure 26. Pelves in left lateral view. *a, Leptobrachium hasselti,* MCZ 22626, × 3; *b, M. monticola nasuta,* MCZ 22640, × 1.8; *c, Pelobates cultripes,* UMMZ S-2631, × 3; *d, Macropelobates osborni,* AM 6252, × 1.8. Dashed line indicates restoration.

it is related to the latter genus, it also resembles pelobatines in many features. Examination of the various species of *Eopelobates* might indicate to some workers that several genera rather than one are included. *E. hinschei* and *E. anthracinus,* for example, might be referred to two genera if the other species were unknown. Hecht (1963, p. 23) has already suggested that *E. grandis* is "probably another genus distinct from the European [*E. anthracinus*]," and that at least two types of pelobatids are present in the Geiseltal frog fauna. As far as the latter case is concerned, after examining the Geiseltal collection in 1965 and 1967, I found no reason to recognize species additional to *E. hinschei,* although it is possible that I overlooked another form. *E. grandis* is similar in body proportions to *E. anthracinus,* as is *E. guthriei* in frontoparietal shape; these three species seem to form a short-skulled lineage. *E. bayeri* and *E. hinschei,* on the other hand, are relatively long-skulled forms, at least as far as proportions of nasal and frontoparietal are concerned. These two lineages appear to be linked by the distinctive squamosal shape of *E. hinschei* and *E. guthriei* on the one hand, and of *E. anthracinus* and *E. bayeri* on the other. In addition, *E. grandis, E. bayeri,* and *E. hinschei* show similarities of the frontoparietal border. The rather granular dermal sculpture pattern of *E. grandis* is superficially different from the open, ridged pattern of *E. hinschei,* but these intergrade through the other species.

The list of similarities given at the beginning of this paper indicates that for the present it is best to include all of these species in one genus; I believe that no useful purpose would be served by distinguishing the two lines within *Eopelobates* generically. The situation is somewhat similar to that in the *Scaphiopus-Spea* complex, and the morphological differences are nearly of the same order. Since most recent workers who have dealt with both recent and fossil forms have preferred only subgeneric distinction of *Scaphiopus* and *Spea* (Zweifel, 1956; Kluge, 1966), retention of the fossil species in one genus, *Eopelobates,* makes the internal classification of pelobatids more consistent. I prefer not to apply subgeneric distinctions to the two inferred fossil lineages without better knowledge of the record, however.

Adaptation and Intrafamilial Classification

In the final analysis of *Eopelobates,* it is clear that its position cannot be defined in terms of the archetypal and hierarchial series of stages proposed by Noble (1924, p. 9) and utilized by Parker (1929, p. 280).

Kluge's statements on generic definition (1966, p. 18) are pertinent to this problem. Rather than giving unnecessary emphasis to either a "classical morphotype" or an "adaptive" approach, he shows that both approaches produce similar results when treated in an evolutionary context incorporating the pattern of variation displayed by the organisms. *Eopelobates* or any other fossil must, of course, be defined on observable, hence morphological criteria. Yet when it is compared with living representatives whose adaptive characteristics may be more fully known, its own adaptive features may be assessed more meaningfully.

In this context, it is a frog having a tendency towards elongated limb and body segments, especially those of the distal hind limb. This produces an adaptation, similar to that of many species of *Rana* (e.g. *R. pipiens*), as a semiaquatic, saltatorial animal. It is even more similar in proportions to the living *Discoglossus* (also semiaquatic and saltatorial) than it is to the other discoglossids, *Bombina* and *Alytes*, which are more terrestrial and have more compact, pelobatine proportions (Figs. 24, 25).

The fused dermal skull casque is reminiscent of such fossil discoglossids as *Latonia* and *Zaphrissa* and may have been derived from some common ancestor, although as noted at the beginning of this paper it may be a separately derived condition. The thin anterior lamina on the scapula also occurs in discoglossids, although the scapula is much shorter.

Eopelobates can thus be viewed as a primitive pelobatid, and in the light of the characters discussed above, one not easily relegated to either of the living subfamilies. In an evolutionary approach, subfamilial or other taxonomic boundaries are by definition arbitrary. *Eopelobates* is intermediate between megophryines and pelobatines, and *Macropelobates* connects it with the latter. The Megophryinae are defined by characters not found in fossils (Beddard, 1907), but should these become known for *Eopelobates*, it is possible that the fossil genus would show an intermediate condition here as well. For the sake of convenience, distinction between the two subfamilies can be maintained by the presence or absence of a spade; in this context *Eopelobates* becomes the most pelobatine member of the Megophryinae; *Macropelobates* the most megophryine of the Pelobatinae.

An alternative position would be to place *Eopelobates* in a monotypic subfamily ancestral to the two Recent subfamilies. I have emphasized the position of *Eopelobates* as intermediate between the two currently recognized groups, yet I have also attempted to show that it is more closely related to the Megophryinae. In part the decision is determined by one's philosophy of classification. I prefer to emphasize the megophryine relationships here, but it is quite possible that more detailed study of the Czechoslovakian specimens will show that there is sufficient justification for separate subfamily status of *Eopelobates* (Špinar, in litt., 1969).

THE PELOBATINAE

The most primitive known spadefoot toad is *Macropelobates osborni* Noble (1924), from the Hsanda Gol Formation of Mongolia. Originally believed to be of late Oligocene age, the associated fauna is now thought to be at about the boundary between early and middle Oligocene (Mellett, 1968).

Recent preparation of the unique specimen of *Macropelobates* has shown features that further confirm its primitive pelobatine position, and which must be discussed before considering spadefoot evolution as a whole.

Macropelobates osborni Noble 1924

The skull of *Macropelobates* is somewhat dislocated, but it is possible to restore its general proportions with fair certainty. The

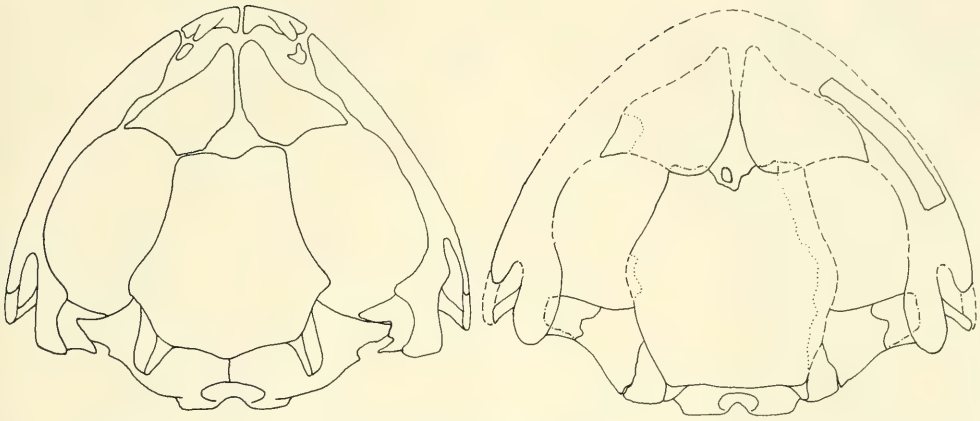

Figure 27. Left, skull roof of cleared and stained *Pelobates syriacus balcanicus*, MCZ 50690, × 3; right, restoration of skull roof of *Macropelobates osborni*, AM 6252, × 1.8. Dashed line = restoration; dotted line = broken bone edge; dotted and dashed line = bone border covered by other bone in life.

breadth across the back of the skull can be determined since the dorsal part of the squamosal is present and the otoccipital is complete laterally. Most of the ethmoid is present, and, by comparison with all other pelobatids, it seems clear that the skull did not exceed 30–32 mm in length. The suggested proportions are compared with (e.g.) *Pelobates syriacus* in Figure 27.

The dorsal surface of the skull is flattened or slightly concave, as in most megophryines, including *Eopelobates*. The rounded tympanic process of the squamosal is pelobatine rather than *Eopelobates*-like. There is a posterior process on the maxilla (the latter bone is forced into the left orbit and was called the ethmoid by Noble) indicating the probable presence of a quadratojugal and hence of a complete maxillary arcade. The smooth and essentially complete borders of the frontoparietal and the posterior part of the squamosal indicate that no postorbital bone bridge was present between these two bones. As in *Pelobates cultripes*, *P. fuscus*, and small *P. syriacus*, there is an opening on the midline between frontoparietals and nasals, and, as is common in *P. cultripes*, a small separate nubbin of dermal ossification is present. The nasals are missing but the facet for the posterior border is present on the left side of the ethmoid, and a faint impression occurs medially on the ethmoid. The medial part of the posterior border of the otoccipital is expanded posteriorly as in *Pelobates*, and the tip of the prootic part of the otoccipital is narrow, also as in *Pelobates*. In general shape and lack of a thickened and projecting anterior process, the ethmoid is like *P. cultripes* and *P. syriacus* rather than *P. fuscus* or *Scaphiopus* (Figs. 5, 7). A moderately developed turbinal fold is present as in *Pelobates*, and in anterior view the ethmoid is similar to that of *P. cultripes* (Fig. 3).

The tarsus is completely pelobatine (Fig. 28). The tibiale and fibulare are about the same length as the radius, as in *P. cultripes*, *P. fuscus*, *Leptobrachium*, and some primitive *Megophrys*, rather than being significantly longer as in *Eopelobates* or shorter as in some *Scaphiopus* and *P. syriacus*. The tibiale is strongly expanded distally as in all pelobatines. A sickle-shaped, enlarged prehallux (spade) is present and closely bound to a large proximal element or pretarsal. Lateral to this is a large centrale 1, followed by distal tarsal 1. The well-ossified tarsus of megophryines includes a large fused distal tarsal 2 + 3, even in small

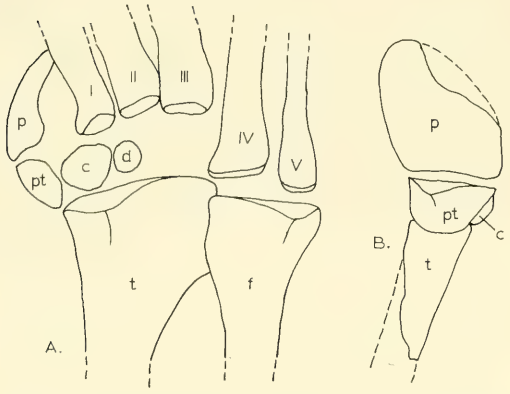

Figure 28. *Macropelobates osborni*, AM 6252; *a*, plantar view of right ankle; *b*, lateral view of spade; × 3. I–V = metatarsals; c = centrale 1; d = distal tarsal 1; f = fibulare; p = prehallux; pt = pretarsal; t = tibiale.

individuals. In pelobatines the latter bone does not ossify, but the other bones occur in all species. In *Scaphiopus* (*Spea*) and *S.* (*Scaphiopus*) *couchi* the pretarsal and prehallux fuse.

The tibiofibula is shorter than the femur as in all pelobatines.

The length from the dorsal border of the acetabulum to the anterior tip of the ilium approximately equals that of the femur. This is greater ilial elongation than is common in pelobatines but such proportions do occur in large *Pelobates cultripes*. The ischial projection posteriorly is more as in *Pelobates* than in *Eopelobates* or *Megophrys* (Fig. 26).

The sacral diapophyses are expanded to about the length of 4.5 presacral vertebrae as in *Pelobates*. The forward inclination of the transverse processes of the posterior vertebrae is not quite so extreme as in *Pelobates* and is more like that of most *Megophrys* and *Eopelobates*.

The urostyle is elongate, exceeding the length of the sacral diapophyses and about equalling or exceeding the length of the skull. In this feature it is in general agreement with that of megophryines and, to a lesser degree, *Scaphiopus;* it is unlike that of *Pelobates,* contrary to the statement of Zweifel (1956, p. 12).

The flatness of the skull surface, the lesser inclination of posterior transverse processes, and the elongated urostyle are the only features that distinguish *Macropelobates* from *Pelobates.* These features are similar to those of *Eopelobates* and some *Megophrys,* and are probably primitive for the Pelobatidae. The other features of the skeleton relate *Macropelobates* closely to *Pelobates* (especially *P. cultripes*) and to the new *Scaphiopus* described below; this serves to clarify and expand Noble's concept of this genus as differing only slightly from the modern forms. Zweifel (1956) and Parker (1929) have cited a similarity of proportions of *Eopelobates, Megophrys,* and *Macropelobates.* As Figures 24, 25, and 29 show, the latter is clearly on the pelobatine growth curve. Only the elongated urostyle can be cited as a megophryine proportional feature.

Macropelobates seems to represent an early member of the pelobatines, in diagnostic ways characteristic of that group, but possessing a few features relating the spadefoots more closely to the megophryines. It is closest, however, to *Pelobates,* especially *P. cultripes,* and can only be separated from it by the megophryine primitive characters noted above and by the absence of the enlarged dermal covering of the squamosal and the squamosal-frontoparietal bridge.

Pelobates

The fact that *Macropelobates* seems to have its closest relationships to *P. cultripes*[1] probably indicates the primitive position of the latter species. Gislén (1936) has already considered *P. cultripes* primitive on the basis of size, parasphenoid teeth, and frontoparietal-squamosal connection. The first two characteristics, however, are of little value. The frontoparietal-

[1] Here, as elsewhere in this discussion unless otherwise stated, the conditions of the very closely related *Pelobates varaldii* (Pasteur and Bons, 1959) are as in *P. cultripes.*

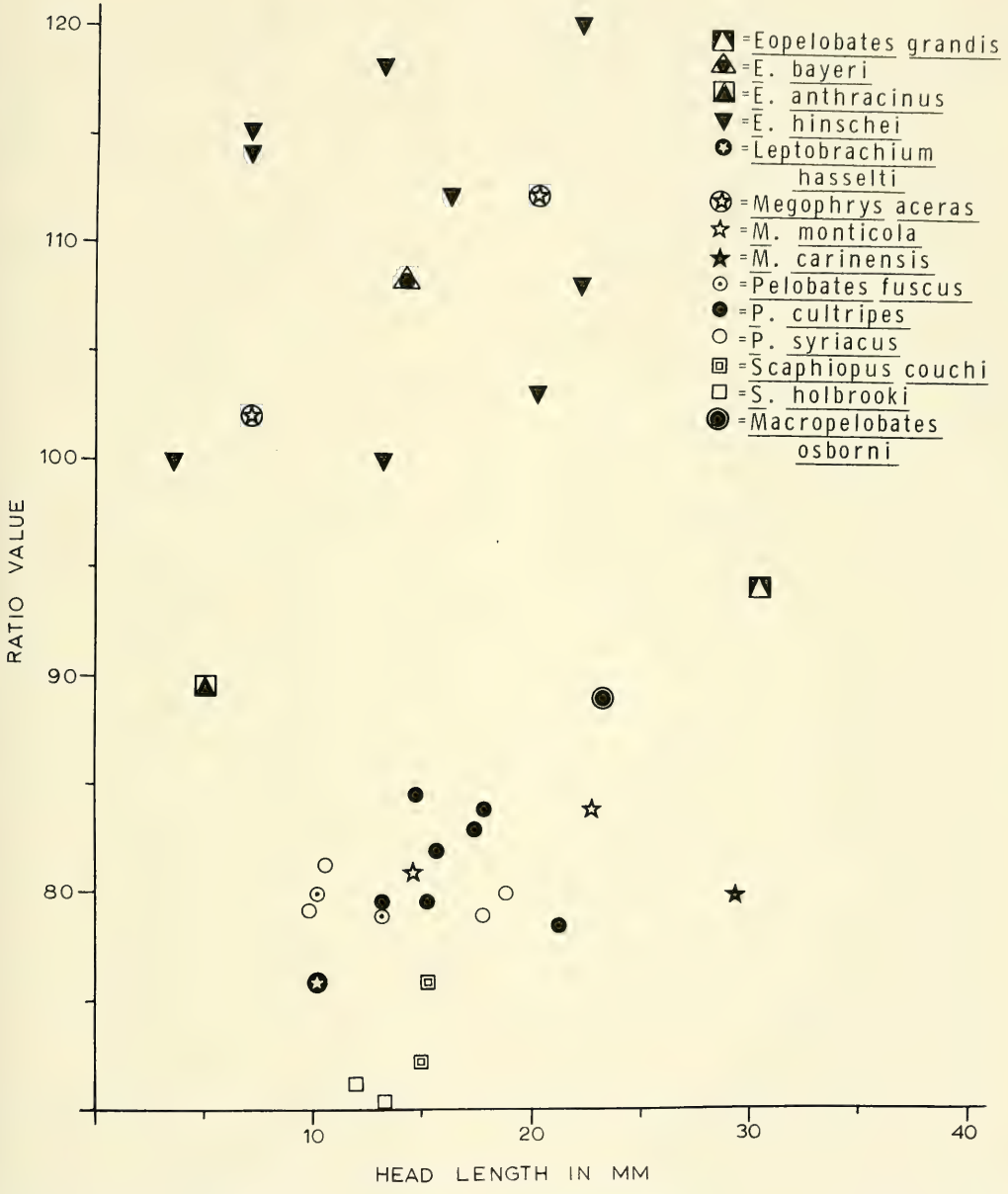

Figure 29. Ratio of tibiofibula-femur length to head-body (skull-urostyle) length plotted against head length for various pelobatids.

squamosal connection was shown to be a secondary condition in the discussion of anatomical features at the beginning of this paper.

Pelobates syriacus is most closely related to *P. cultripes*. Both *P. cultripes* and *P. syriacus*, as well as the primitive *Scaphiopus holbrooki* and *S. skinneri* described below, have an ethmoid with little ossification of the anterior process, but *P. fuscus*

has developed a complex anterior process similar to that of the specialized *Scaphiopus couchi.* While *P. fuscus* has an unusual prootic foramen (Kluge, 1966, p. 13; Fig. 16, this paper), *P. cultripes* and *P. syriacus* have one of more open, megophryine type as in Figure 16b. *P. syriacus* has a tibiale and fibulare shorter than the radius, a condition advanced over that of *S. holbrooki* and more like that of the specialized *S. couchi.* Thus both *P. syriacus* and *P. fuscus* appear to be advanced over *P. cultripes,* although in different ways and to different degree; *P. fuscus* is the more specialized of the two former species. Zweifel (1956) has suggested that *P. fuscus* is most like *S. holbrooki,* but as the description (see below) of the new Oligocene *Scaphiopus* material shows, *Macropelobates* is probably phyletically closer to the ancestral spadefoot than is the relatively specialized *P. fuscus.*

Miopelobates robustus (Bolkay, 1913)

Pelobates robustus Bolkay (1913), from the Lower Pliocene of Hungary, was described on the basis of maxillae, premaxillae, angular, thyroid process of hyoid, and ilium, all fragmentary. Bolkay noted that the maxillae were not completely covered with osteoderms, the anterior part being relatively smooth and separated from the sculptured posterior area by a "bifurcated furrow" (1913, p. 219, pl. 11, fig. 1).

Wettstein-Westersheimb (1955) described *Miopelobates zapfei* on the basis of frontoparietals, nasals, maxillae, sacra, urostyles, and vertebrae from the Middle Miocene fissures near Neudorf, Czechoslovakia. The material is dissociated although some of it, designated "Typen" by Wettstein (1955, p. 812), may be from the same individual. The paired frontoparietals are in contrast with those of *Pelobates, Macropelobates,* and *Eopelobates bayeri.* The nasals are compact and *Scaphiopus*-like in appearance, although there was apparently a dorsal exposure of the ethmoid. The maxillae differ from those of *Eopelobates bayeri* in lacking a lobed squamosal process and sinuous posterior border. The expanded squamosals are most like those of *Pelobates cultripes.* The relatively straight borders of the sacral diapophyses are more as in *Pelobates* than in *Eopelobates.*

The peculiar smooth anterior portion of the maxillae, the suborbital sculptured area, and the bifurcated furrow (for facial blood vessels and nerves) separating these two areas are clearly visible on Wettstein's specimens (1955, pl. 2, fig. 3a) and there seems little doubt that Wettstein's species *zapfei* is a synonym *of robustus.* The very *Pelobates*-like ilium that Bolkay associated with *P. robustus* suggests that *Miopelobates* is a pelobatine. This is supported by the configuration of the squamosals, the sacra, and the nasals as noted above. Because of the paired frontoparietals and the peculiar ossification pattern, this species is retained in Wettstein's genus *Miopelobates.* Kluge (1966, p. 16) allied *Miopelobates* with the Megophryinae, but for the above reasons I believe it to have been a spadefoot. It may have been a somewhat aberrant offshoot from the ancestral *Pelobates* type, and may be near *P. cultripes* as indicated by the expanded squamosals.

Młynarski (1961) has cited a possible occurrence of *Miopelobates* from the Lower Pliocene of Poland; this is very likely in view of its now recognized occurrence in the Lower Pliocene of Hungary.

Scaphiopus

Since both Zweifel (1956) and Kluge (1966) recently discussed the evolution of the North American spadefoots, discussion here will be limited to the pertinence of the new Oligocene *Scaphiopus* described below to their scheme of spadefoot diversification.

Scaphiopus skinneri, n. sp.

Type: FAM 42920, complete skull and vertebral column, left scapula, right coracoid, left? thyroid ossification.

Referred specimens: FAM 42921, one left and one right frontoparietal, both fragmentary, and a partial vertebral column with adherent tibiofibular fragment.

Etymology: Patronym for Mr. Morris Skinner, Frick Laboratory, American Museum of Natural History, who collected the type specimen in 1950.

Locality: Leo Fitterer Ranch, Sect. 7, T 137 N, R 97 W, 13 miles South, 8 miles west of Dickenson, Stark County, North Dakota.

Horizon: First banded zone, 15 feet above base of channel deposits, Unit no. 6A (Skinner, 1951, p. 53).

Age: Middle Oligocene, Orellan (European equivalent = Helvetian).

Preservation: The skull, vertebral column and girdle elements are associated and in almost natural position. The skull has been separated from the vertebral column for study. The skull is well preserved on the right side, but on the left, part of the posterior region of the squamosal and the left frontoparietal are lost. The left otoccipital had been dislocated at the time of burial (probably when the squamosal and frontoparietal were lost) but has been prepared free and replaced in its natural position. Otherwise the skull is undistorted and uncrushed. The atlas and the neural arch of the fourth vertebra are lost, as are the tips of the transverse processes of all vertebrae.

Description: In posterior view the skull roof appears essentially flat but is slightly depressed medially. The occipital canal opens just medial to the prominent paroccipital process. The foramen magnum is a flattened oval; its apex is directed dorsally. The occipital region is well preserved, although the left frontoparietal, left stapes, and lateral edges of the otoccipital are missing. The otoccipitals extend laterad to form the border of the fenestra ovalis. Dorsally they articulate with the frontoparietal and ventrally with the parasphenoid, which is excluded from the fenestra ovalis. The foramen for the ninth and tenth cranial nerves opens prominently just lateral to the large, rounded occipital condyles. The paroccipital process has a prominent boss on its lateral tip, just lateral to the frontoparietal and the occipital canal. The prootic is notched laterally, and forms the medial border of the foramen for the maxillomandibular branch of the trigeminal nerve. The stapes is just posterior and dorsal to this foramen, and has a forked head fitting into the anterodorsal part of the fenestra ovalis. A large opercular space remains, but if a calcified operculum was present, it has been lost. Since such delicate structures as tooth crowns, septomaxillae, and stapes remain, it is likely not to have been present. The prominent descending suspensorium is formed by the pterygoid medially, and the squamosal laterally, which clasp between them the well-developed quadrate.

Dorsally the premaxillae are unsculptured; the right bone is well preserved but the nasal process of the left is missing. The nasals are prominently sculptured and complete except for their pointed anterior processes above the nasal openings. They articulate on the midline where they form a slight depression, and also laterally with the maxillae. There is no open groove or unsculptured area in the nasomaxillary suture. The frontoparietals are also sculptured and have a prominent postorbital projection (broken except on FAM no. 42921a, Fig. 30). Anteriorly they articulate with the nasals but leave a small trapezoidal area of the ethmoid uncovered on the midline. Posteriorly their borders are rounded, curving into the postorbital projection. A tiny, pointed, and unsculptured process of the frontoparietal extends onto the paroccipital process. Maxillae and squamosals are also completely covered by dermal sculpture; the latter articulate firmly with the former but there is no connection or process of squamosal to or toward the frontoparietals. The tympanic process of the squamosal is prominent and rounded, and a broad prootic process covers the tip of the otoccipital. The latter

Figure 30. *Scaphiopus skinneri*, n. sp. *A–E*, dorsal, right lateral, ventral, anterior, and occipital views of skull; *F–G*, vertebral column, dorsal and ventral views; *H*, scapula, coracoid, and thyroid process ossification; FAM 42920, × 2. *I*, right frontoparietal, anterior end broken, FAM 42921a; × 2.

bone is exposed to its tip on its posterior end.

Laterally the maxillae are deep and sculptured over all their surface except for a narrow band immediately dorsal to the teeth. The latter are pedicellate, and most of the narrow, spatulate crowns are preserved. The rounded tympanic process of the squamosal extends almost to the occipital condyles posteriorly and is notched ventrally for the tympanic membrane. No quadratojugal is present, although there is, on the lateral surface of the quadrate, a tiny projection that may represent its fused remnant.

In palatal view the vomers have strong processes anterior to the choanae, there are small tooth patches medially, the bones do not meet on the midline, and slim lateral processes to the palatines almost reach the pterygoids. The palatines are completely fused to the maxillae. The ethmoid has strong lateral processes, and well-developed concavities behind the vomers indicate a prominent "turbinal" fold. The anterior tip of the ethmoid is broken away. The pterygoids have a long suture with the maxillae and end in small unossified spaces separating them from the vomers.

The parasphenoid wings clasp the pterygoids laterally; anteriorly the cultriform process lies smoothly on the ethmoid without developing a channel, and posteriorly there are well-defined crests for nuchal and retractor bulbi muscles, and for the eustachian tubes.

The prootic foramen is elongated and open anteriorly; its dorsal and ventral borders are approximately parallel. The oculomotor and optic foramina are not outlined in bone.

The mandibles are broken away posteriorly. Anteriorly the symphysial (mentomeckelian) bones are present, separated from the prearticulars by unossified spaces and clasped by the dentaries.

In anterior view the premaxillae are well preserved but loosely attached. On the right, the ascending process contacts the small septomaxilla. The anterior process of the ethmoid is broken away but was apparently not thickened; a well-defined capsular process with a prominent turbinal fold is visible.

The atlas is missing, as is the neural arch of the fourth vertebra. The vertebrae are procoelous, and, posteriorly, the ninth (sacral) vertebra has well-defined, hatchet-shaped diapophyses. The main postsacral foramina are relatively small, and there appears to have been a smaller second pair as well as considerable webbing (about as in Zweifel, 1956, fig. 19g). The urostyle is broken off but the narrowness of the remaining portion and the presence of two pairs of postsacral foramina indicate without much question that it was fused with the sacrum.

The scapula, coracoid, and ossified thyroid cartilage are all robust but display no unusual characteristics. The disarticulated vertebral column (FAM 42921c) is similar to that of the type.

Discussion: Scaphiopus skinneri, in possessing the following characters, is clearly referable to the subgenus *Scaphiopus*: (1) presence of squamoso-maxillary contact, (2) widely emarginate prootic foramen, (3) absence of frontoparietal fontanelle, (4) extensive dermal skull, (5) probable absence of calcified operculum, (6) presence of pterygoid process of maxilla, (7) presence of palatine, (8) large size. These characters are as given by Kluge (1966, p. 19) except that the condition of the operculum (his character no. 6) is reversed in his table for the two subgenera, although given correctly in the text (1966, p. 10).

In general skull proportions, *Scaphiopus skinneri* is similar to the most primitive living species, *S. holbrooki*. It has a broader skull when compared with length of presacral column: 1/2 skull breadth = 5.5 presacrals as opposed to 4.5 presacrals in a random sample of *S.* (*Scaphiopus*) at hand, although this relationship may be the result of large size of the fossil. It resembles *S.*

holbrooki in orbitotemporal opening, although its orbit is not relatively as large (see Fig. 15d, e). As shown by the referred frontoparietals, the postorbital projection is rounded and relatively far forward as in S. *holbrooki*. However, the tympanic process of the squamosal is longer, the posterior extent of dermal bone on squamosal and frontoparietal is greater than in any modern pelobatine, and the skull as a whole is slightly more flattened than in S. *hammondi*. In these characters it resembles *Eopelobates, Macropelobates,* and *Pelobates cultripes*. The tendency in other species of *Scaphiopus* and in *Pelobates* is to develop a more domed skull, although that of *P. cultripes* is flatter than it is in any other living pelobatine. The persistence dorsally of a small area of ethmoid not covered by dermal bone is also a character reminiscent of *Eopelobates, Pelobates fuscus,* and *P. cultripes*. Usually in all *Scaphiopus* (*Scaphiopus*) and in most *P. syriacus,* the dermal covering of the frontoparietals fills this space.

The vertebral column is not unusual except that the second vertebra has the condyle of the atlas fused to it and is hence bicondylar. This fusion is irregular, however, and does not appear to be the usual condition, although it was certainly functional in this individual. A variety of articulations have been noted in pelobatids; Boulenger (1908) found both opisthocoely and procoely in *Megophrys,* and Griffiths (1963) found free intervertebral discs in an adult *Megophrys major* as did Noble (1926). My observations are in accord with theirs, and in addition, I have found free intervertebral discs in a large, cleared and stained adult *Pelobates syriacus* (MCZ 50690). Thus, no significance should be attached to the bicondylar fossil vertebra; all the other vertebrae are procoelous. The length (expansion) of sacral diapophyses in this specimen is equal to the length of nearly three presacral vertebrae, and I have found this to be the case in all individuals in my sample of *Scaphiopus* (*Scaphiopus*), contrary to the statements of Kluge (1966, p. 17) and Zweifel (1956, Table 1).

The girdle elements and thyroid cartilage ossification resemble those of Recent S. (*Scaphiopus*) and are in about the same size proportion to the skull.

Scaphiopus skinneri is a primitive *Scaphiopus* as shown by the generally more depressed skull, relatively small orbit, flat skull roof, large rounded tympanic process of the squamosal, low squamosal angle (50°; Griffiths, 1963, fig. 2, p. 248 and see section on this character-state at beginning of this paper), posterior extent of dermal bones on frontoparietal, and dorsally exposed ethmoid. Yet, as noted above, it possesses all of the characteristics of the subgenus *Scaphiopus*. In orbitotemporal proportions, degree of expansion of the anterior process of the ethmoid, and short quadrate process of the squamosal, it resembles the most primitive living *Scaphiopus, S. holbrooki*.

It is also similar to *Macropelobates* in the large, rounded tympanic process of the squamosal and the shape of the posterior part of the frontoparietal. These are probably primitive pelobatine characters.

Eopelobates guthriei resembles *Scaphiopus* in having a relatively short skull, strongly concave posterior border of the prootic part of the otoccipital, long narrow prootic foramen, and relatively great posterior extent of nasals. It is perhaps the closest to the spadefoot line of any known megophryine. Possibly the two groups had their common ancestor in the Paleocene or perhaps even in the Cretaceous. The fact that the well-defined *Scaphiopus skinneri* occurs in the early Oligocene indicates that the spadefoot line is at least as old as Eocene, and perhaps older; S. *skinneri* also occurs in the early Oligocene of Saskatchewan; this material is being described by Dr. J. Alan Holman.[1] As

[1] Holman, 1969. Quart. Jour. Florida Acad. Sci. **31**:273–289; received after this paper went to press.

with the living *S. holbrooki, S. skinneri* and probably all primitive *Scaphiopus* were associated with deciduous forests and an essentially humid warm-temperate or subtropical climate (in the sense of Dorf, 1959). The development of the *Spea* complex was probably correlated with the semiarid open woodland scrub and grasslands that were beginning to develop in midcontinental North America by the middle and late Oligocene (Dorf, 1959, p. 189). This is essentially the picture already set forth by Zweifel (1956, p. 41) and supported by Kluge (1966, p. 21).

SPECIES REMOVED FROM THE PELOBATIDAE

Zaphrissa eurypelis Cope 1866, described from the Middle Oligocene lignite beds of Rott, near Bonn, Germany, is usually considered a discoglossid (Friant, 1960). Kuhn (1938, p. 20) synonymized it with *Pelobates* on the basis that Wolterstorff (1929, p. 931) believed it to be "identisch mit *Pelobates decheni* Tr.," but later (Kuhn, 1962) replaced it in the Discoglossidae. Friant (1960) suggested that it might be a juvenile of *Latonia*, a giant discoglossid from the Miocene deposits at Oeningen. The type specimen of *Zaphrissa* was recently rediscovered (Baird, 1970). It has ribs, opisthocoelous vertebrae, a relatively large atlas, a very short scapula, and a double condyle on the urostyle. These characters in combination indicate that the specimen is discoglossid. It has a well-developed dermal skull casque rather like that of *Pelobates cultripes*. The frontoparietal fenestra cited by Cope, and used as an indication of juvenility by Friant (1960), is actually an area where the dermal bone has been broken away before burial, although such a fenestra does occur occasionally even in such a heavily encrusted skull as that of *P. cultripes* (UMMZ S-2630).

I have not seen the material of *Pelobates decheni* noted above, but if Wolterstorff was correct, then the material is incorrectly referred to *Pelobates* and the proper name for this animal would be *Zaphrissa decheni*.

Nevo (1956) gave a preliminary notice of fossil frogs from the early Cretaceous of Israel and stated that the specimens displayed some pelobatid features. Griffiths (1963, pp. 276, 282, 283) later referred to these specimens as pelobatids. A more detailed paper by Nevo (1968) shows these specimens to be members of the Pipidae.

EVOLUTION AND ZOOGEOGRAPHY OF THE PELOBATIDAE

If the late Cretaceous Lance Formation specimens from Wyoming are properly referred to *Eopelobates* (p. 315), then this earliest pelobatid was associated with a humid, subtropical, coastal plain environment in North America (Estes, 1964). The paucity of the Cretaceous record in Europe precludes knowledge of a possibly wider distribution of the group. In any case, the extensive epicontinental seas characteristic of the Northern Hemisphere Cretaceous would probably have hindered or prevented such movement. Holarctic continental connections seem not to have been re-established until the late Paleocene (Russell, 1964), and strong intercontinental faunal similarities persisted until the end of early Eocene time. By this time, *Eopelobates guthriei* was already established in North America and this form may be near the point of divergence of the spadefoot line. *E. guthriei* was associated with a climate essentially like that of the late Cretaceous of Wyoming. Although there is floristic evidence for a period of cooling at the beginning of the Cenozoic (Dorf, 1959), much of the lower vertebrate fauna already established by late Cretaceous time persisted through the Paleocene in Wyoming (Estes, 1962).

Not later than late Paleocene or early Eocene time, *Eopelobates* must have achieved a Holarctic distribution. By mid-

Eocene time, it was well established in Europe in the swamps of the Geiseltal in what was an essentially tropical environment (Krumbiegel, 1959, p. 116). The Geiseltal species, *E. hinschei,* was the most specialized member of the group in that it had developed relatively long posterior limb segments like those of mainland populations of the Recent *Megophrys aceras,* but since the latter is montane the ecology of the two forms must have been quite different. These proportions, in *E. hinschei,* were probably adaptations for an amphibious existence much like that of some species of *Rana,* e.g. *R. pipiens,* which remains on moist banks and uses its long limbs for jumps either for food or to regain the safety of the water.

Although in squamosal shape *Eopelobates hinschei* shows resemblance to *E. guthriei* in North America, it seems to have been the ancestor of a relatively long-headed European line that persisted until at least the middle Miocene.

Eopelobates was also present in North America during the middle Eocene, although the remains are fragmentary. A subtropical climate still persisted in the midcontinental area at this time, but a slight cooling effect has been noted (Dorf, 1959). North American and Eurasian *Eopelobates* must have been pursuing separate evolutionary paths at this time, for faunal interchange was now relatively restricted.

The next record of *Eopelobates* is in the early Oligocene of North America. This animal, *E. grandis* (Zweifel, 1956), is the largest known member of the genus. It resembles *E. guthriei* in having a short, wide frontoparietal, and was almost certainly an autochthonous element.

Early Oligocene also saw the appearance of the first spadefoot toads: *Scaphiopus skinneri* is more primitive than, but is closely related to, the most primitive living species, *S. holbrooki.*

Climatic changes were beginning to take place at this time (early-middle Oligocene); *Eopelobates grandis* and *Scaphiopus skinneri* probably lived in a warm-temperate rather than subtropical climate (Dorf, 1959; Clark et al., 1967). The warm temperate flora extended into Alaska (Dorf, 1959) and there was a period of strong faunal interchange (Simpson, 1947). A form close to *Pelobates* was already established in the early Oligocene of Belgium (Hecht and Hoffstetter, 1962). It is possible that spadefoots were derived from *Eopelobates* in the Eocene in North America, or even in the Paleocene. Skull proportions of American *Eopelobates* suggest a closer approach to spadefoot proportions than do those of the long-headed European forms.

E. anthracinus indicates that the short-headed lineage was also present in Europe, however, where it appeared in the middle Oligocene of Germany. It is a relatively short-headed form bearing frontoparietal similarities to the Eocene North American *E. guthriei.* Its squamosals resemble those of the somewhat later *E. bayeri* of Czechoslovakia (*cf.* Figs. 8, 12, 13, 19, 20), while the body proportions appear similar to those of *E. grandis* (Fig. 24). This may indicate that it was derived from short-headed North American populations that migrated to Europe not later than the early Oligocene, and probably earlier. It might be assumed that its body proportions are the result of its small size, but even small members of *E. hinschei* have body proportions related to those of the large specimens (Fig. 29). On the basis of the short, emarginated frontoparietal, I prefer the first alternative.

At the end of the Oligocene, *Eopelobates bayeri* appears in Central Europe. It persists into the middle Miocene, and is closely related to the Eocene *E. hinschei,* and is also a long-headed form. It probably lived under subtropical conditions in the late Oligocene, which became more warm-temperate in the Miocene (Dorf, 1959). These changing conditions seem to have been related to the disappearance

of *Eopelobates* in Europe by middle Miocene time. *Pelobates*-like fossils are present in France in the late Miocene (Hecht and Hoffstetter, 1962).

The same deteriorating climatic conditions that caused the eventual extinction of *Eopelobates* were favorable to the continued development of the essentially warm-temperate spadefoot line. The first known spadefoot, *Scaphiopus skinneri*, occurs at a latitude transitional at that time between subtropical and warm-temperate conditions (Dorf, 1959). It is probable that this transitional climate was the site of original evolution of the spadefoot type, and that they spread northward from the transition into Temperate regions.

The Eocene of North America was a time of the gradual rise of the midcontinental region. Mountain building activity associated with this rise exposed granitic rocks, whose erosion produced the sandy soils preferred by spadefoots, as well as by other burrowing animals. These soils were (and are) used by spadefoots as a retreat from aridity and because of ease of burrowing. Not only did the mountain building itself cause the developing aridity, but it also produced the soils favoring the fossorial adaptation.

Because the early and middle Oligocene *Scaphiopus skinneri* was already a primitive but well differentiated member of the North American spadefoot line, the Holarctic spread of the spadefoot group must have been *no later* than the late Eocene, when faunal similarities (principally mammalian) indicate that migration was taking place again between Old and New Worlds. The Holarctic radiation was also possible during the early Eocene, and because of the spadefoot resemblances of *Eopelobates guthriei* I favor this alternative (Fig. 31). Since we have no Eocene record of the spadefoots, another possible alternative is that *Scaphiopus* originated in Asia after the early Eocene spread of the ancestral type. In view of the present inadequate fossil record, the simplest explanation is an autochthonous origin of *Scaphiopus*.

Macropelobates, the primitive *Pelobates*-like spadefoot, appears in Asia by the middle Oligocene. Although it is closer to *Pelobates*, in certain features *Macropelobates* shows some similarities to *Scaphiopus skinneri*, demonstrating some intermediacy between Old and New World forms. The ancestral *Pelobates* populations probably spread westward into Europe no later than early Oligocene, if the material noted by Hecht and Hoffstetter (1962) is indeed *Pelobates* or its ancester. Populations of the genus extended through Northern Europe into the Iberian Peninsula, and evolved into a group ancestral to *P. cultripes* and *P. syriacus*. At the eastern edge of its range, this ancestral group probably formed northern and southern sections on each side of the late Cenozoic Aralocaspian sea-lake (Gislén, 1936; Gignoux, 1955); the modern species had probably evolved by Miocene time. During the Pleistocene, the advancing ice sheets restricted *P. cultripes* and *P. syriacus* to the Iberian Peninsula and Asia Minor, respectively. *P. fuscus*, derived probably from northern populations of *P. syriacus*, remained in Europe wherever the advancing ice sheets permitted, and as Gislén (1936) has already noted, again spread widely over northern Europe during the thermal maximum. Fossils of *Pelobates* have been found in various localities in Europe (see Młynarski, 1961) from at least as far back as the early Pliocene, and other possible occurrences go back to early Oligocene (Hecht and Hoffstetter, 1962). These remains have not been studied carefully by anyone who had an adequate sample of all three Recent species; such a study would be very helpful towards understanding the diversification of the European spadefoots. It seems clear, however, that *P. fuscus* is the most recent and specialized of the three species and that it is not directly related to *Scaphiopus holbrooki*, its ecological

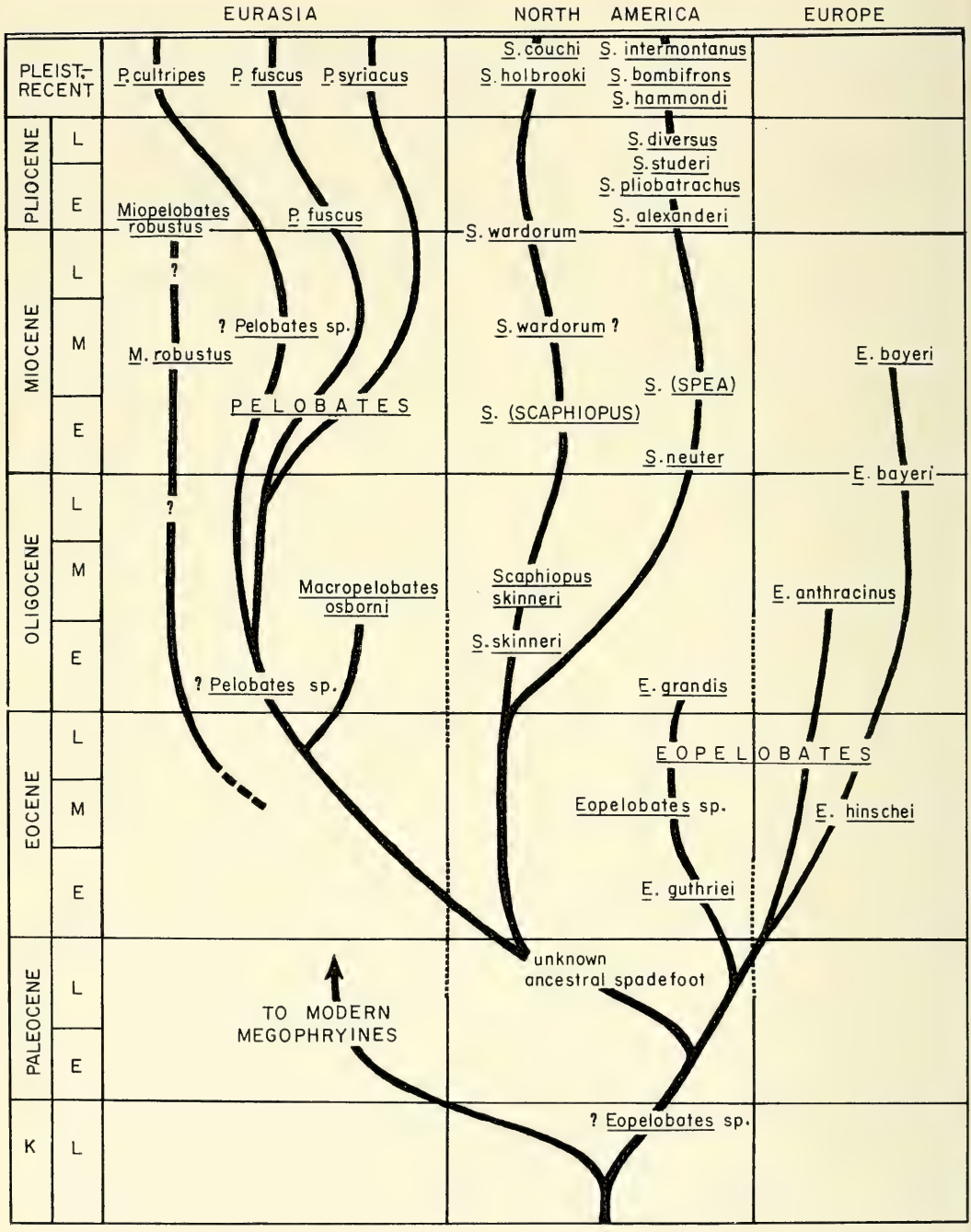

Figure 31. Temporal, geographical, and inferred phyletic relationships of pelobatids. On the vertical lines separating the continental areas, the times of major faunal exchange (based primarily on mammals; Simpson, 1947) are indicated by broken lines.

equivalent in North America. The findings of this study support Zweifel's contention that *Scaphiopus* and *Pelobates* had a common fossorial ancestor, and that *Macropelobates* is close to that ancestor although too late in time. The patterns of diversification within *Scaphiopus* suggested by Kluge (1966) and Zweifel (1956) are consistent with the known fossils.

The position of the modern megophryines is not directly clarified by this study. It is a diverse group and seems to include animals spanning the range of body proportions found in other pelobatids. Because of the peculiar nature of their dermal ossification, their primitive ethmoid, and the similarity of nasal-frontoparietal relationships to the early Cenozoic long-headed European lineage of *Eopelobates*, I consider them to be of very ancient origin from a common stock with *Eopelobates*. As noted in several places above, the primitive megophryine genus *Leptobrachium* is the closest to *Eopelobates* of any of the modern forms, yet the resemblance is not especially strong. *Eopelobates* may have been in existence in the late Cretaceous, and since all Cenozoic members show pelobatine features not found in modern megophryines, I believe that their common ancestor cannot have been later than the late Cretaceous. *Leptobrachium* and its relatives were probably tropical differentiates of the ancestral pelobatids. Whether or not the resemblance between the long-skulled European *Eopelobates* and the Recent southeast Asian forms implies an origin of pelobatids in the Old World Tropics is conjectural. Zweifel (1956, p. 15) has properly emphasized the caution necessary in making such inferences. Darlington (1957) favors the origin of many groups in the Old World tropics and such an origin has been often assumed by authors dealing more specifically with amphibians (e.g. Noble, 1924). Yet it is perfectly plausible to imagine a common ancestor of megophryines and pelobatines living in relatively high-latitude Holarctic tropics of the late Mesozoic, and differentiating into tropical *Leptobrachium*-like forms (their descendants remaining still in present day tropics), tropical and subtropical *Eopelobates* (now extinct) and the temperate geographical replacements of the latter, the pelobatines.

In this latter scheme, *Leptobrachium* and its relatives became restricted to the Old World tropics during the early Cenozoic, and subsequently differentiated into a number of island and montane (temperate) forms. *Eopelobates* diversified into mainly subtropical environments, but also extended into tropical areas (*E. hinschei*). With the progressive restriction of high latitude tropical climates during late Cenozoic time, some warm-temperate forms developed into pelobatines, adapting progressively to increasing aridity in both Old and New Worlds by developing a burrowing habitus. They now have a complementary, Holarctic distribution. *Eopelobates* itself was perhaps unable to compete with more successful ecological analogues that were becoming widespread by the Miocene, such as some species of *Rana*, and therefore became extinct.

APPENDIX I:
LIST OF RECENT COMPARATIVE MATERIAL

Numbers refer to measured specimens, Figures 24, 25. Numbers in parentheses indicate that more than one specimen is listed under a given museum number.

Pelobatidae

Megophryinae

1. *Leptobrachium hasselti,* MCZ 22626, Borneo.
2. *Megophrys monticola nasuta,* MCZ 22640, Borneo.
3. *M. m. nasuta,* MCZ 19756, Sumatra.
4. *M. monticola,* AM 24786, Java.
5. *M. lateralis,* AM 23549, Kuang China.
6. *M. aceras,* AM 23964, Burma.
7. *M. ?aceras,* MCZ 23436, Burma.
8. *M. ?aceras,* MCZ 23437, Burma.
9. *M. carinensis,* AM 23965, Burma.
10. *M. robusta,* MCZ 25735, Thailand.

11. *Scutiger mammatus,* MCZ 17422, Szechuan, China.

Pelobatinae

1. *Pelobates cultripes,* UMMZ S-2629, no data.
2. *P. cultripes,* UMMZ S-2630, no data.
3. *P. cultripes,* UMMZ S-2631, no data.
4. *P. cultripes,* BM 682, Spain.
5. *P. cultripes,* BM 233, Spain.
6. *P. cultripes,* S-002 (Coll. Špinar), France.
7. *P. cultripes,* S-001 (Coll. Špinar), France.
8. *P. varaldii,* MCZ 31970, Morocco.
9. *P. syriacus balcanicus,* MCZ 50690, Romania.
10. *P. fuscus,* MCZ 1012, Italy.
11. *P. fuscus,* MCZ 1013, Italy.
12. *P. fuscus,* MCZ 1353, Italy.
13. *P. fuscus,* MCZ 1012-b, Italy.
14. *P. fuscus,* MCZ 1013-c, Italy.
15. *Scaphiopus h. holbrooki,* MCZ 25577, Massachusetts (2).
16. *S. h. holbrooki,* MCZ 17420–1, Massachusetts (2).
17. *S. h. holbrooki,* MCZ 17418–9, Massachusetts (2).
18. *S. h. holbrooki,* MCZ 28786, Florida.
19. *S. h. holbrooki,* AM 58003, Florida.
20. *S. holbrooki hurteri,* AM 44244, Texas.
21. *S. couchi,* AM 14478, Baja California.
22. *S. couchi,* MCZ 64374, Arizona (cleared and stained).
23. *S. couchi,* AM 56284, Arizona.
24. *S. couchi,* AM 57641, Arizona.
25. *S. couchi,* MCZ 3079, Texas.
26. *S. couchi,* MCZ 6710, Texas.
27. *S. couchi,* MCZ 44335, Mexico.
28. *S. couchi,* MCZ 44336, Mexico.
29. *S. intermontanus,* AM 16918, Utah.
30. *S. intermontanus,* AM 16916, Utah.
31. *S. bombifrons,* MCZ 32912, Texas.
32. *S. bombifrons,* MCZ 32913, Texas.
33. *S. bombifrons,* MCZ 32911, Texas.
34. *S. bombifrons,* MCZ 32914, Texas.

Discoglossidae (only specimens used in Fig. 25 listed)

35. *Discoglossus pictus,* MCZ 3196, Corsica.
36. *Alytes obstetricans,* MCZ 904, France.
37. *Bombina orientalis,* MCZ 19722, Korea.
38. *Barbourula busuangensis,* MCZ 25656, Philippines.

Extensive comparison has been made with many specimens of other families of frogs too numerous to mention here. All specimens examined (other than those noted in this appendix from other institutions) are in the collection of the Museum of Comparative Zoology, Harvard University. A list of specimens available in the skeletal collection is available on request from the Curator of Reptiles and Amphibians.

REFERENCES CITED

Baird, D. 1970. Type specimen of the Oligocene frog *Zaphrissa eurypelis* Cope, 1886. Copeia, 1970, no. 2, pp. 384–385.

Başoğlu, M., and S. Zaloğlu. 1964. Morphological and osteological studies in *Pelobates syriacus* from Izmir Region, Western Anatolia. Senckenb. Biol. **45:** 233–242 (R. Mertens Festschrift).

Beddard, F. E. 1907. Contributions to the knowledge of the anatomy of the batrachian family Pelobatidae. Proc. Zool. Soc. London, **1907:** 871–911.

Bolkay, S. J. 1913. Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial Periode. Jahrb. kgl. ungar. Geol. Reichsanst. **20:** 217–230.

Boulenger, G. A. 1908. A revision of the Oriental pelobatid batrachians (genus *Megalophrys*). Proc. Zool. Soc. London, **1908:** 407–430.

Clark, J., J. R. Beerbower, and K. K. Kietzke. 1967. Oligocene sedimentation, stratigraphy, paleoecology, and paleoclimatology in the Big Badlands of South Dakota. Fieldiana: Geol. Mem. **5:** viii + 158 pp.

Cope, E. D. 1866. On the structures and distribution of the genera of the arciferous Anura. Journ. Philadelphia Acad. Nat. Sci. (N. S.) **6:** 67–112.

Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals. New York: John Wiley and Sons, xi + 675 pp.

Dorf, E. 1959. Climatic changes of the past and present. Contr. Mus. Paleon. Univ. Michigan, **8:** 181–210.

Estes, R. 1962. Late Cretaceous and early Cenozoic lower vertebrate faunas in North America. Program Geol. Soc. Amer. Natl. Meetings, **1962:** 46a.

———. 1964. Fossil vertebrates from the late Cretaceous Lance Formation, eastern Wyoming. Univ. Calif. Publ. Geol. Sci. **49:** 1–180.

———. 1969. A new fossil discoglossid frog from Montana and Wyoming. Mus. Comp. Zool., Harvard Univ., Breviora No. **328:** 1–7.

Estes, R., M. Hecht, and R. Hoffstetter. 1966. Paleocene amphibians from Cernay, France. Amer. Mus. Novit., **2295:** 1–25.

Friant, M. 1960. Les batraciens anoures. Caractères ostéologiques des Discoglossidae d'Europe. Acta Zool. **41:** 113–139.

Gignoux, M. 1955. Stratigraphic Geology. San Francisco: W. H. Freeman Co., (trans. G. Woodford), xvi + 682 pp.

Gislén, T. 1936. On the history of evolution and distribution of the European pelobatids. Zoögeographica, **3**: 119–131.

Griffiths, I. 1963. The phylogeny of the Salientia. Biol. Rev. **38**: 241–292.

Hecht, M. K. 1959. Amphibians and Reptiles. *In*: McGrew, P. O. et al., The Geology and Paleontology of the Elk Mountain and Tabernacle Butte Area, Wyoming. Bull. Amer. Mus. Nat. Hist., **117**: 117–176.

———. 1963. A reevaluation of the history of the frogs, II, System. Zool. **12**:20–35.

Hecht, M., and R. Hoffstetter. 1962. Note préliminaire sur les amphibiens et squamates du Landenien supérieur et du Tongrien de Belgique. Bull. Inst. Roy. Sci. Nat. Belgique **38**: 1–30.

Inger, R. F. 1966. The systematics and zoogeography of the Amphibia of Borneo. Fieldiana: Zoology, **52**: 1–402.

Kluge, A. G. 1966. A new pelobatine frog from the Lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. Los Angeles County Mus. Contr. Sci. **113**: 1–26.

Krumbiegel, G. 1959. Die tertiäre Pflanzen- und Tierwelt der Braunkohle des Geiseltales. Die Neue Brehm-Bücherei, Heft 237, Wittenburg Lutherstadt: A. Ziemsen Verlag, 1–156.

Kuhn, O. 1938. *In*: Fossilium Catalogus, I: Animalia, Pars **84**: Stegocephalia, Urodela, Anura. 98 pp.

———. 1941. Die Eozänen Anura aus dem Geiseltale. Nova Acta Leop. (n. f.) **10**: 345–376.

———. 1962. Die vorzeitlichen Frösche und Salamander, ihre Gattungen und Familien. Jahrb. Ver. Vaterl. Naturkde. Württemberg. **1962**: 327–372.

Mellett, J. S. 1968. The Oligocene Hsanda Gol Formation, Mongolia: A revised faunal list. Amer. Mus. Novit., **2318**: 1–16.

Mertens, R. 1923. Beiträge zur Kenntnis der Gattung *Pelobates* Wagler. Senckenbergiana, **5**: 118–128.

Młynarski, M. 1961. Płazy (Amphibia) z Pliocenu Polski. Acta Palaeont. Polonica, **6**: 261–282.

Nevo, E. 1956. Fossil frogs from a Lower Cretaceous bed in southern Israel (central Negev). Nature (London), **178**: 1191–1192.

———. 1968. Pipid frogs from the early Cretaceous of Israel and pipid evolution. Bull. Mus. Comp. Zool., Harvard Univ. **136**: 255–318.

Noble, G. K. 1924. A new spadefoot toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidae. Amer. Mus. Novit., **132**: 1–15.

———. 1926. An analysis of the remarkable cases of distribution among the Amphibia, with descriptions of new genera. Amer. Mus. Novit., **212**: 1–23.

Parker, H. W. 1929. Two fossil frogs from the Lower Miocene of Europe. Ann. Mag. Nat. Hist., (10)**4**: 270–281.

Pasteur, G., and J. Bons. 1959. Les batraciens du Maroc. Trav. Scient. Chérifien, Ser. Zool., **17**: xvi + 240 pp.

Russell, D. E. 1964. Les Mammifères paléocènes d'Europe. Mem. Mus. Natl. d'Hist. Nat., Paris (n. s.) **13**: 1–324.

Skinner, M. F. 1951. The Oligocene of Western North Dakota. *In*: Bump, J. D., ed., Guide Book, Fifth Field Conference, Soc. Vert. Paleon., Mus. Geol. So. Dakota School Mines Tech., Rapid City, So. Dakota.

Simpson, G. G. 1947. Holarctic mammalian faunas and continental relationships during the Cenozoic. Bull. Geol. Soc. America, **58**: 613–688.

Špinar, Z. V. 1952. *Eopelobates bayeri*, nová zaba z ceských tretihor. Sbornik Ustredního Ustavu Geologického, **19**: 457–488, English summary.

———. 1967. Neue Kenntnisse über den stratigraphischen Bereich der familie Palaeobatrachidae Cope, 1865, ibid., **42**: 217–218.

Westphal, F. 1958. Die Tertiären und Rezenten Eurasiatischen Riesensalamander (Genus *Andrias*, Urodela, Amphibia). Palaeontographica., **110**: 20–92.

———. 1967. Erster Nachweis des Riesensalamanders (*Andrias*, Urodela, Amphibia) im europäischen Jungpliozän. Neues Jahrb. Geol. Paläont., Monatsh. **1967**: 67–73.

Wettstein-Westersheimb, O. 1955. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March (ČSR.). Amphibia (Anura) et Reptilia. Sitz.-Ber. Österr. Akad. Wiss., Math.-Natl. Kl. **164**: 801–815.

Wolterstorff, W. 1929. Über fossile Frösche aus der Papierkohle von Burgbrohl (Laacher See), Jahrb. Preuss. Geol. Landesanstalt. **49**: 918–932.

Zweifel, R. G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationship to fossil and Recent forms. Amer. Mus. Novit., **1762**: 1–45.

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Other Publications.

Bigelow, H. B., and W. C. Schroeder, 1953. Fishes of the Gulf of Maine. Reprint, $6.50 cloth.

Brues, C. T., A. L. Melander, and F. M. Carpenter, 1954. Classification of Insects. $9.00 cloth.

Creighton, W. S., 1950. The Ants of North America. Reprint, $10.00 cloth.

Lyman, C. P., and A. R. Dawe (eds.), 1960. Symposium on Natural Mammalian Hibernation. $3.00 paper, $4.50 cloth.

Peters' Check-list of Birds of the World, vols. 2–7, 9, 10, 12, 14, 15. (Price list on request.)

Turner, R. D., 1966. A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia). $8.00 cloth.

Whittington, H. B., and W. D. I. Rolfe (eds.), 1963. Phylogeny and Evolution of Crustacea. $6.75 cloth.

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THE GALAXIID FISHES OF NEW ZEALAND[1]

R. M. McDOWALL[2]

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ABSTRACT

Fourteen species in the family Galaxiidae are recognized from New Zealand, three fewer than in previous works. These are placed in two genera —*Galaxias* and *Neochanna*—as follows: *Galaxias argenteus* (Gmelin), *G. fasciatus* Gray, *G. postvectis* Clarke, *G. brevipinnis* Günther, *G. vulgaris* Stokell, *G. maculatus* (Jenyns), *G. usitatus* McDowall, *G. gracilis* McDowall, *G. divergens* Stokell, *G. paucispondylus* Stokell, *G. prognathus* Stokell, *Neochanna burrowsius* (Phillipps), *N. apoda* Günther, and *N. diversus* Stokell. This arrangement of taxa differs from previous arrangements in that lacustrine populations formerly known as *G. lynx* Hutton and *G. koaro* Phillipps are treated as synonyms of *G. brevipinnis*, *G. anomalus* Stokell is found to be a synonym of *G. vulgaris* and, although formerly placed in *Galaxias*, *Neochanna burrowsius* is regarded as showing much greater similarity to and affinity with the other neochannoid species and is accordingly placed in *Neochanna*.

Study of samples of the migratory juveniles of the diadromous species (*G. argenteus*, *G. fasciatus*, *G. postvectis*, *G. brevipinnis*, and *G. maculatus*) showed that although clear diagnostic characters for the juveniles of these species do not emerge, it is possible to distinguish species in mixed samples by means of modal differences in length at migration, head length, and body depth.

The diadromous species were found to have numerous small to moderate-sized eggs, to spawn mostly in the autumn and early winter, to spend larval and early juvenile life in the sea, and to

[1] This paper is based on a thesis presented to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the Ph.D. degree.

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migrate into fresh water during the subsequent spring. *G. usitatus* and *G. gracilis* have forsaken the marine migratory habits (because of landlocking), but have numerous small eggs. The remaining seven species have few, larger eggs, spawn mostly in the winter and spring, and complete their entire life histories in fresh water.

The correlation between egg size, egg number, and life history pattern suggests selective advantage in having many small eggs, in species living initially in productive, marine plankton, and fewer, larger eggs in species living in flowing fresh water and not subject to the same type of dispersal away from the natal habitat.

There is a very obvious relationship between range and life history pattern—those species with marine life history phases are widespread in the New Zealand region and may occur on offshore islands and also in other, more distant land areas (Australia, South America). These species tend to have easily determined phylogenetic relationships with species outside the New Zealand region. Species restricted to fresh water have a much more restricted range and have largely cohesive distribution patterns, which can be mostly explained simply by known changes in New Zealand's geomorphology.

The age of the New Zealand galaxiid fauna is unknown. The family seems to have evolved in the Australasian region, since about 90 per cent of the species occur there. Phylogenetic relationships with the Retropinnidae and Aplochitonidae and a common origin for the three families in some early Northern Hemisphere salmoniform stock are suspected.

Phylogenetic relationships between Australian and New Zealand species can in many cases be established, and this, together with known marine life history phases, indicates that the New Zealand fauna is derived by transoceanic dispersal. The East Australian ocean current seems to provide a suitable mechanism for dispersal from Australia to New Zealand.

Although the New Zealand freshwater fish fauna is very small, there is no evidence that the present fauna represents only a fragment of a formerly larger fauna, reduced by marine transgressions that occurred during the early and mid-Tertiary, or by the glaciations of the Pleistocene. Though the fauna is small, and though the Galaxiidae represent a large proportion of the fauna, the family shows little evidence of radiation to fill the New Zealand freshwater habitats. Galaxiids are mostly solitary, stream dwelling, benthic, invertebrate feeding predators. They seem to show considerable sensitivity to alterations in the nature of the stream catchment and its vegetation cover.

The galaxiid fauna is easily and naturally divisible into a series of small species groups. *G. argenteus, G. fasciatus,* and *G. postvectis* are clearly closely related to each other, and to *G. truttaceus* in Australia. *G. brevipinnis* is very similar to, perhaps conspecific with *G. weedoni* in Tasmania, and is also probably ancestral to *G. vulgaris. G. maculatus* is common to Australia, New Zealand, and South America, and gave rise in New Zealand to *G. usitatus* and *G. gracilis. G. divergens, G. paucispondylus,* and *G. prognathus* form a very compact species group of an origin at present undetermined. *N. burrowsius, N. apoda,* and *N. diversus* are similarly very closely related and are perhaps derived from the Tasmanian neochannoid species, *G. cleaveri* and *G. anguilliformis.*

INTRODUCTION

The fishes of the family Galaxiidae are mostly small and scaleless, more or less benthic in habit, with rounded trunks and somewhat depressed, broad heads. Nearly all the species are secretive and solitary and have thick, fleshy fins. Some species are nocturnal, with free-ranging, pool-dwelling habits, and may exhibit some deepening of the trunk. A few species have mid-water shoaling habits, and these tend to have membranous fins and a more slender form.

The family Galaxiidae is very widespread in the Southern Temperate Zone, species occurring in Australia, New Zealand, South America, and South Africa, as well as on many islands in the vicinity of these land areas. Species abundance is greatest in Australia and decreases eastwards to New Zealand, South America, and South Africa in the pattern described by Fell (1962: 761). One species, *G. maculatus* (Jenyns), is found in Australia, Tasmania, Lord Howe Island, New Zealand, Chatham Islands, Chile, Patagonia, and the Falkland Islands, and is one of the most widely dispersed species of freshwater fish.

The family Galaxiidae is currently considered to belong to the order Salmoniformes (Greenwood et al., 1965: 394), comprising, with the families Aplochitonidae, Retropinnidae, and Salangidae, the suborder Galaxioidei. These four families are considered to constitute a distinctive radiation within the Salmoniformes. Var-

ious of the three southern families—Galaxiidae, Retropinnidae, Aplochitonidae—have at some time been related to the salmonoid or the haplomous fishes (Regan, 1909; Berg, 1940; Chapman, 1944; Gosline, 1960); the present consensus agrees that they have very definite salmonoid affinities (Weitzman, 1967; McDowall, 1969).

From the beginnings of galaxiid taxonomy late in the 18th century, the family has been a difficult and confused one. The morphology of the New Zealand species is plastic, and in many localities and some species groups, active speciation is occurring. The failure of earlier workers to take into account the rather distinctive juveniles, and the allometric growth that may succeed the juvenile stages, has led to repeated descriptions of some species. Lack of knowledge of the life history patterns and their relation to dispersal has resulted in description of fishes from apparently isolated localities as new. Repetitive description of well-defined species due to ignorance of earlier descriptions or mistaken identity has added to the problems, and confusion in the application of existing names has been considerable; e.g., Powell (1869), discussing the young stages of some *Galaxias* species, called them "smelt"—properly *Retropinna* in New Zealand—and published a figure that is clearly *G. maculatus* (Jenyns), labeling it *G. fasciatus* Gray.

Apart from a small paper by Hutton (1896) and Regan's (1905) revision of the whole family, the works of Stokell (1945, 1949) were the first serious attempt to define the New Zealand galaxiid species, and for the first time it became possible to identify adults of most of the species occurring in New Zealand. As a result of these and later papers by Stokell (1954, 1959b, 1960) and one by the writer (McDowall, 1967a), there are currently 17 galaxiid species recognized from New Zealand.

Studies of a New Zealand fishery based on species of *Galaxias* (McDowall, 1964b, 1965a, 1968b) showed that more meristic data and clearer diagnostic characters should be sought for adequate identification of some of the species, especially in their juvenile stages. Subsequent collections of many large samples of all the New Zealand species from a wide range of localities also suggested that there were some irregularities in their taxonomy. As a result of the present review, the number of species recognized is reduced to 14.

An attempt to determine species groups, phylogenetic patterns, and the evolution of the New Zealand galaxiid fauna is long overdue. It is also time that an attempt be made to relate the New Zealand fauna to the galaxiid faunas in Australia and South America. It is the objective of this study to attempt a synthetic analysis of the New Zealand Galaxiidae, to examine the manner in which galaxiid fishes appear to have invaded New Zealand's fresh waters and speciated there, and to determine the phylogenetic relationships of the species. Unfortunately, the systematics of the Australian and South American galaxiid faunas are not well known; studies of the species in these two areas will be necessary before the desired synthesis of the whole family can be accomplished.

MATERIALS AND METHODS

Material examined. A large collection of New Zealand Galaxiidae was studied, much of which was collected during a study of the biology of *G. maculatus* (McDowall, 1968b) or on specific field trips to collect certain species. Further material was collected by technicians at the Fisheries Research Division of the New Zealand Marine Department, and this was supplemented by samples in the collection of the New Zealand Dominion Museum. *Neochanna burrowsius* is a rare species that is difficult to collect, and my samples of this species were small; examples in the fish collections of the University of British Columbia and the National Museum of Canada were also

Figure 1. New Zealand place names—regions and physiographic features mentioned in text.

studied. For most species, large series were examined from a broad range of geographical localities. I have not listed in detail the material examined in the study, but in the distributional data for each species an asterisk is inserted by localities from which specimens were examined for meristic or morphometric data. The identifications of species from each locality are my own, except for a number reported by Fisheries Research Division biologists and technicians.

Museum abbreviations. In the listing of type specimens, the institutions at which the types are held are indicated by the following abbreviations:

AMS	Australian Museum, Sydney, Australia.
BMNH	British Museum (Natural History), London, England.
CMCNZ	Canterbury Museum, Christchurch, New Zealand.
DMNZ	Dominion Museum, Wellington, New Zealand.
GMUO	Geology Museum, University of Otago, Dunedin, New Zealand.
MCZ	Museum of Comparative Zoology, Cambridge, Mass., U. S. A.
MNHNP	Museum National d'Histoire Naturelle, Paris, France.
NZMD	New Zealand Marine Department, Fisheries Research Division, Wellington, New Zealand.
USNM	United States National Museum, Washington, D. C., U. S. A.

Sampling techniques. Galaxiid fishes are usually secretive, occupy deep cover, and are fast swimming; many species occur in very rapid, turbulent water. Thus they are usually difficult to capture. The principal tool used for collection was a small, backportable electric fishing machine, which was used in all waters except estuaries where high salinities sometimes rendered it inoperable because of high water conductivity. Also, in some very pure mountain streams conductivity was very low and the effectiveness of the machine greatly reduced. The normal running time for one set of batteries—a pair of six-volt motorcycle batteries—was one and a half to two hours, although this depends on water conductivity. With two sets of batteries it was possible to spend a full day in the field without recharging. The effectiveness of the machine was greatest in shallow water, up to about 24 inches, and for the capture of solitary, cover-dwelling species. However, using the machine in conjunction with small seine nets, shoaling species were easily captured in large numbers. Paralyzed fish were usually retrieved with small metal gauze dip nets, but in torrential streams it was necessary to place a barrier, like a large dip net, a bag net, or a small seine across the stream flow, and chase the fish downstream towards the barrier with the electrode. For capturing shoaling fishes, a small, five-foot, one-man seine was constructed from fine-mesh mosquito netting strung between two bamboo poles; a length of light chain was used to weigh down the lower edge of the net.

Captured fish were immediately placed in a pail of water containing a narcotic—usually chlor-butol, occasionally "MS 222." Narcotizing the fish as they were caught prevented distortion due to asphyxiation and allowed long collection runs in the field without delays for fixing specimens. Whenever possible, the fish were fixed in the field, in shallow plastic photographic trays. The fish were spread out in the trays with minimal overlap and sufficient 10 per cent formalin poured on to cover but not float them. They were bottled when they had begun to harden. By this simple expediency, the difficulty of working with bent, twisted, and otherwise distorted specimens was almost completely avoided, and in general, the specimens were in excellent condition. After fixation for four or five days in formalin, the fish were washed for a similar period in several changes of tap water and transferred to 40 per cent isopropyl alcohol for storage.

Measurements and counts. Methods of measurement used were largely those de-

scribed by Hubbs and Lagler (1947: 13–15, figs. 3–5), in a few cases adapted to the particular morphological characteristics of the fishes studied. In most cases, measurements were taken with needle point dividers, although in large species vernier calipers were found to be more effective. In general, dimensions were determined to the nearest half millimeter. In small fish, and in measuring small dimensions, usually those less than 15 mm, and whose reference points are well defined, measurements were estimated to the nearest quarter millimeter. Frequently, accuracy of this degree is not warranted since the reference points are not clearly defined, and variations in body flexure at fixation and types of preservative used modify the body dimensions to an extent that makes accuracy of a quarter of a millimeter, and sometimes half a millimeter, quite meaningless.

Measurements were taken as follows: total length—either length to caudal fork (L.C.F.), or if the caudal is rounded, to posterior extremity of fin (T.L.); standard length (S.L.); body depth at vent (B.D.V.) —used instead of greatest body depth because the latter is greatly affected by sexual maturity and distension of the stomach after feeding; depth of caudal peduncle (D.C.P.); length of caudal peduncle (L.C.P.); predorsal length (Pre-D.); preanal length (Pre-A.); length of bases of dorsal and anal fins (D.F.B. and A.F.B.); maximum length of dorsal and anal fins (D.F.M. and A.F.M.); pectoral fin length (Pec.); pelvic fin length (Pel.); pre-pelvic length (Pre-Pel.); pectoral-pelvic length (Pec.-Pel.); head length (H.L.)—measured to edge of opercular membrane; head depth (H.D.)—an uncertain measurement, but taken vertically at the ridge across the nape which represents the posterior margin of the cranium, the position of which can be determined by running the finger forwards across the top of the head; head width (H.W.); snout length (Sn.L.); postorbital head length (P.O.H.L.); interorbital width (Io.W.)—fleshy interorbital; diameter of eye (D.E.)—horizontal fleshy eye diameter, not bony orbit; length of upper jaw (L.U.J.); length of mandible (L.M.); width of gape (W.G.).

The following structures were counted: fin rays in the dorsal, caudal, anal, pelvic, and pectoral fins; vertebrae; gill rakers on the first arch; branchiostegals; pyloric caeca. Counting fin rays in galaxiid fishes presents a minor problem, since a variety of types of soft rays occurs. As in all the salmonoid fishes, procurrent rays are present in the dorsal, anal, and caudal fins. Hubbs and Lagler (1947: 9) recommended the inclusion of these rays in the counts of the dorsal and anal fins of salmonoids. In the Galaxiidae, such a procedure is a problem, since the anteriormost rays are usually deeply embedded in the opaque, fleshy fin bases and accurate counts are impossible without staining. Use of alizarin stain techniques showed that in the dorsal and anal fins there are from one to five of these rays, varying in size from a tiny, little-ossified splint, to a strongly-ossified but unbranched and unsegmented ray. Accordingly, the counts given in the subsequent descriptions are, in all cases, of segmented rays, whether branched or not. This procedure, which enables accurate and standardized counts, is more or less equivalent to the principal ray count, although sometimes a segmented, unbranched ray is counted, which does not quite reach to the distal margin of the fin, as it should to be counted as a principal ray. In the paired fins, the situation is a little simpler and more stable. Occasionally one unbranched but segmented ray is present in the medial border of the pectoral and pelvic fins, and this was counted, together with the larger branched rays. The small, unsegmented splintlike ray, more rarely present in these fins, was not counted.

Vertebral counts were taken as excluding the urostylar vertebra and hypural plate. Their inclusion would increase the count by one or two, depending on whether the

urostylar elements were fused or not; the condition was found to be variable. All branchiostegals, including those which do not have a definite attachment to the hyoid arch, were counted. Gill rakers were counted in the conventional manner, the raker at the angle between the epibranchial and ceratobranchial, which does not associate with either bone, being counted with the lower limb.

All counts were made using a dissecting stereomicroscope. In many cases, samples were sufficiently large to allow preparation of cleared, stained skeletal preparations. X-rays were also used extensively for vertebral counts.

Clearing and staining. During the early part of the study, the potassium hydroxide clearing technique of Hollister (1934) was employed. Later, the clearing method developed by Taylor (1967), in which trypsin is utilized for the digestion of body tissues, was used. The principal advantage of this method is that the problem of explosion and distortion of fish and the fragmentation of old specimens is largely avoided. In addition, clearing is accomplished more rapidly than in other techniques, and distorted, asphyxiated specimens are often partially relaxed.

SYSTEMATICS

Family Galaxiidae

The family Galaxiidae was formed by Müller (1844) to contain the genus *Galaxias* Cuvier, 1817. Osteological study is becoming imperative for understanding the relationships of the species within the family, as well as among the Galaxiidae and the Retropinnidae and Aplochitonidae, and the relationships of the three families with the broader sphere of the isospondylous fishes. The present synopsis hopefully forms an initial basis for determining the limits of the family.

Diagnosis. Medium-sized to small fishes (3–60 cm) with 0–3 rudimentary to well-developed pyloric caeca. Both gonads developed, although the left may be larger than the right, ovaries gymnoarian. Urinogenital aperture on a papilla set in a postanal depression. Sexes similar, male nuptial tubercles not present, but in many species sensory tubercles present on the head and pectoral fins in both sexes. All the species except one are believed to breed in fresh water, the exception in river estuaries. Some species are confined to fresh water, either lacustrine or fluviatile, others are amphidromous with marine juveniles.

Scales lacking, lateral line well developed, an accessory lateral line present dorsolaterally in some species.

Pelvic fins abdominal, 4-8 rays, usually 7, or fin absent. Caudal fin emarginate to rounded, rarely forked, usually 16 principal rays (14 branched), procurrent rays well developed along caudal peduncle and anterior to dorsal and anal fins, dorsal and anal fins originate well back on trunk. Vertebrae 37–64, branchiostegals 5–9.

Maxilla partly included in gape, toothless; teeth on premaxilla and dentary uniserial, mesopterygoidal, basihyal, and pharyngeal teeth developed (reduced or absent in *Neochanna*). No supramaxilla; no vomerine teeth.

Parietals large, uniting broadly in a median suture, supraoccipital not in contact with frontals and excluded from foramen magnum. Posterior myodome open. Orbitosphenoid, basisphenoid, and proethmoids absent; supraethmoid and ventral ethmoid present. Posttemporal simple; no mesocoracoid; postcleithrum present or absent. Epipleural and epineural ribs present (except in *Neochanna* and *Nesogalaxias*); neural and haemal arches autogenous, anterior uroneural not fused with terminal vertebra, none of terminal vertebrae upturned. Caudal neural and haemal spines much compressed.

General and diagnostic characters

Fishes of the family Galaxiidae present a varied but distinctive facies. The first observers (Forster, 1778; Bloch and Schneider, 1801) saw a resemblance to the

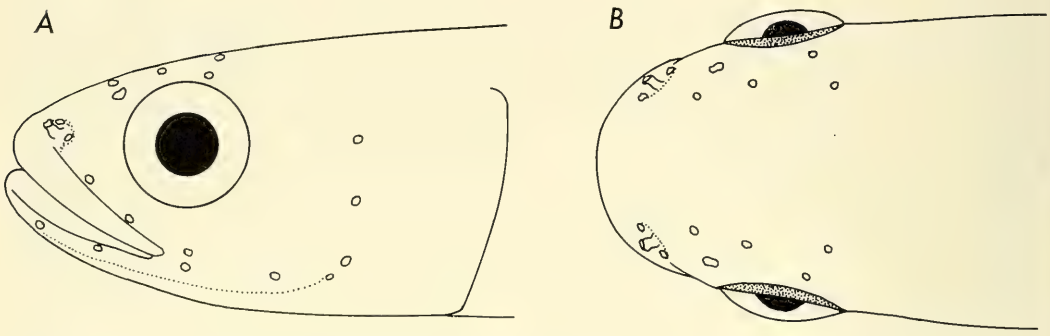

Figure 2. Distribution of laterosensory pores in a generalized galaxiid. A, Lateral head; B, Dorsal head.

Northern Hemisphere pikes (family Esocidae), probably because of the extremely posterior position of the dorsal and anal fins and the long jawed appearance of the single species with which they were acquainted. However, these similarities are superficial. The fishes in the family are scaleless, with thick, highly mucigerous, leathery skins. The head is usually moderately large, with prominent jaws, the upper and lower varying in proportional development so that the lower may protrude, recede, or be equal in length to the upper. Lateral line pores on the head are well developed. In New Zealand representatives, the disposition of these pores is fairly constant, with only occasional individual variations in pore number (Fig. 2). Their disposition can be related to the supra-orbital, infra-orbital, and hyomandibular branches of the lateral line system of the head (see Lagler et al., 1962: 391).

The lateral line is well developed on the trunk from the upper edge of the opercular aperture to the middle of the tail base. It consists of a series of superficial papillae, set in a midlateral furrow, which may be well defined, especially caudally. In some species groups there is a dorsal accessory lateral line along the dorsolateral trunk, evident as a more or less distinct linear series of small, widely-separated papillae from the occiput to about the dorsal fin.

The nostrils are well developed, the anterior one set in a small depression and tubular. In *Neochanna* it is especially well developed, sometimes extending forward beyond the upper lip. The posterior nostril is a simple aperture.

The form of the mouth varies, the profile of the jaws from the ventral aspect varying from deep and narrow, U-shaped, to broad and shallow, with depth much less than breadth (Fig. 3). In the adults of most species, the head, anterior trunk, and pectoral fins and fin bases are covered with small papillae. These are unlike the papillae of the Percidae, which are somewhat horny in nature, or those in the Retropinnidae, which are much better developed and more widespread. They are unusual in that they are present equally in both sexes. Although a directly reproduction-related function cannot be ruled out, the bisexual occurrence of these papillae, apparently in all seasons of the year, suggests a sensory function, which may or may not be related to reproduction. These papillae do not appear to be connected with the lateral line system, as is the case in the head papillae in many fishes. Papillae of this type do not appear to have been discussed in the literature, and their function is at present obscure.

The dorsal and anal fins are positioned posteriorly, and when depressed against the trunk, may overlie the base of the caudal fin; the anal fin is more or less below the dorsal. These fins are variable in their size and shape, usually short-based,

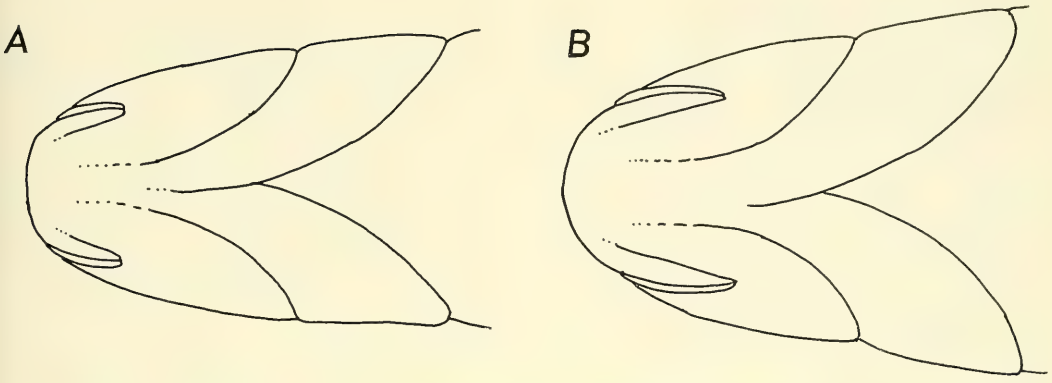

Figure 3. Ventral profile of jaws. A, Broad and shallow—as in *Galaxias divergens*; B, Narrow and U-shaped—as in *G. fasciatus*.

sometimes high and rounded, but in other cases much lower and not extending back much beyond the fin base. The caudal fin varies from well-forked to much-rounded. The pelvic fins are usually rounded in shape and expansive. The pectoral fins are variable in length and position and may be quite high laterally, with the blade of the fin vertical, or low lateroventrally, with the fin lamina more or less horizontal. In most species all the fins are thick and fleshy, especially at the bases.

Teeth are present on the premaxilla, mandible, basihyal, mesopterygoid, the pharyngobranchial of the third, the epibranchial of the fourth, and the ceratobranchial of the fifth branchial arches. The basibranchial plate is toothless. Teeth on all but the basihyal and the pharyngeal bones are uniserial; regularly in some species and in occasional individuals in others, however, there is a tendency for teeth to be displaced laterally from the primary row, appearing biserial. Mesopterygoidal teeth are reduced or absent in the neochannoid species. The teeth are usually conical, but in *Neochanna apoda* the mandibular and maxillary teeth are peculiarly flattened and incisorlike. This condition does not occur in any other galaxiids. In many species the jaw teeth are enlarged laterally as opposing groups of canines. Associated with the toothed bones are unattached, or decumbent teeth, which usually lie freely in the tissues covering the bones.

The structure of the ovaries in the Galaxiidae was described as gymnoarian by Hoar (1957: 289). Kendall (1922: 202) examined the "oviducts" of some salmonoids and concluded that they are shallow, open troughs and not entirely lacking, and that they are not radically different from those of other isospondylous fishes. However, the reduced condition of the oviducts, as in the Salmonidae, persists throughout the salmoniform fishes, and the condition is sufficiently distinct for Hoar to distinguish them from other ovarian types. Breder and Rosen (1966: 614) followed Hoar, stating that in the Galaxiidae and other salmonoids, the "ova pass into the peritoneal cavity and thence through the pores to the exterior." Henderson (1967: 447) concluded that the eggs of Salmonidae are discharged into the abdominal cavity, and that proper oviducts are lacking.

The New Zealand Galaxiidae exhibit considerable morphological plasticity. Most characters were found to vary from species to species, and even usually stable characters, like pelvic and caudal fin ray number, were found to differ in several phylogenetic lines. Stokell (1945:475) considered vertebral number to be the most important taxonomic character. This has

proved to be a useful character, but it is very important to bear in mind the temperature differences that occur along the 900 mile north-south axis of New Zealand—34 1/2 to 47 degrees south latitude—and the effect of temperature on vertebral number.

Apart from vertebral number, important meristic characters included number of caudal, anal, pelvic, and to a lesser extent, pectoral and dorsal fin rays. The number of gill rakers and branchiostegals exhibits interspecific variation.

The most important morphometric characters were the following: length and depth of caudal peduncle, relative positions of the dorsal and anal fins and their basal and maximal lengths, lengths of pectoral and pelvic fins, head length, eye diameter, lengths of upper and lower jaws, width of gape. The development of canine and mesopterygoidal teeth, pyloric caeca, and gill rakers exhibits interspecific variation.

In some species groups, color pattern is diagnostically important: e.g., *G. fasciatus* Gray, *G. argenteus* (Gmelin) and *G. postvectis* Clarke are similar in form but can be separated immediately and reliably by color pattern alone. In other species groups, specific differences are clearly indicated by fundamental differences in the life history pattern: e.g., *G. brevipinnis* Günther has marine or lacustrine whitebait juveniles, whereas *G. vulgaris* Stokell, which is morphologically quite similar, has no whitebait stage.

Most of the taxonomic characters used are completely conventional in ichthyology, but the morphological plasticity of the Galaxiidae results in a considerable diversity of such characters. Some of these are stable and unimportant throughout much of the family although they show significant variation in certain species or species groups (e.g., pelvic fin ray number, snout length), but other characters vary widely throughout the New Zealand members of the family.

Generic classification

Seven generic names have been applied to New Zealand galaxiids. Two of these involve now obvious errors—the use of *Esox* by early workers and the failure of Jenyns (1842: 118) to recognize the previously published genus *Galaxias* when he described galaxiid species in a new genus *Mesites*, a name further invalidated by preoccupation for a genus of beetles (Schoennherr, 1838). These two names are clearly not applicable to galaxiid fishes and present no nomenclatural or taxonomic difficulties.

The type genus for the family is *Galaxias* Cuvier, 1817, for which the type species is *G. fasciatus* Gray, 1842 (see McDowall, 1967b). Günther (1867: 306) described a galaxiid mud-fish in a new genus *Neochanna*, which was distinguished chiefly by the absence of pelvic fins. In 1899, Ogilby placed *G. attenuatus* (Jenyns) in a new genus *Austrocobitis*, distinguished from *Galaxias* by the form of the trunk, the small fins, and the forked caudal. Whitley (1935, 1956a, b) has consistently used *Austrocobitis*, but Stokell (1945: 124) claimed that these characters are widespread amongst divergent groups of galaxiids and that these species do not form a natural grouping. *G. attenuatus* [=*G. maculatus* (Jenyns)] and its New Zealand and Australian derivatives do have characters that set them apart from the rest of the family. However, at present I think that a broad generic revision of the family is necessary, and, thus, that it is inappropriate to make generic changes of this type here.

Scott (1936) proposed a reorganization of the family at subfamilial, generic, and subgeneric levels. In this paper he placed *G. burrowsius* Phillipps in a new genus *Saxilaga*, distinguished by the lack of mesopterygoidal teeth and the presence of pelvic fins (cf. *Neochanna*, which usually lacks both, and *Galaxias*, which has both). Stokell (1945: 129) correctly showed that *G. burrowsius* sometimes has mesopterygoidal teeth, though they are reduced in

size and number. In this paper (p. 134) he listed *Saxilaga* as not recognized and later (1949: 481) described Phillipps's species in the genus *Galaxias*. Phillipps (1940: 39) included this species in the genus *Paragalaxias* Scott, but this is clearly an error since Scott (1936: 87) defined *Paragalaxias* as having the dorsal fin well forward, over the pelvic fins. The allied problem of the validity of the genus *Paragalaxias* need not be considered here.

Scott (1966) reasserted the validity of his generic arrangement of the family. For *Saxilaga*, he noted (p. 250) that "further investigations have shown that certain diagnostic features originally described as absolute probably are not so." He maintained that *Saxilaga* is a good genus for *G. burrowsius* Phillipps, *G. globiceps* Eigenmann, and *G. anguilliformis* Scott, but noted that "if *Saxilaga* is to be maintained, modal and not absolute criteria are to be accepted for these features." He assembled a series of characters that he considered to unite the three species—"elongate body, small eye, small head, reduced number of pelvic fin rays (modally five or six), paired fins short, vertical fins low, squarish, their rays compressed with or without branching . . . . anal continuous or sub-continuous with caudal ridge which is well developed, high, caudal rounded or sub-truncate, fish heavily pigmented . . . . taken collectively, they appear to constitute a significant constellation."

Scott's practice of basing generic divisions on apparently plastic, adaptive, and often widespread characters leads to problems that suggest that such generic divisions are better abandoned. Examination of the distribution of galaxiid genera as he uses them produces the following patterns: *Saxilaga*—Tasmania, New Zealand, South America; *Brachygalaxias* Eigenmann, according to Scott's arrangement—South America, Australia. If we are to use the genus as a collective grouping for species comprising several similar independent radiations from the central stock of the family, then Scott's genera are proper. However, I think that our understanding of the family is better served if we use the taxon to express phyletic relationships. If the species in these two genera are phyletically related, these patterns raise considerable zoogeographic problems, since all the species included belong to groups which, now at least, are found only in fresh water and none of which belong to the much more easily dispersed diadromous species groups. This association of morphological peculiarity with restriction to fresh water has important implications. First, since these species are restricted to fresh water, their ability to disperse is probably lower than that of diadromous species. Second, the fact that they are restricted to fresh water suggests that their common morphological peculiarities may be related to independent development of adaptations to specialized freshwater habitats, as is possibly the case in the mud fishes in Tasmania and New Zealand. I think that some of the similarities that Scott has used to draw species into generic groups are convergent adaptations to similar modes of life (however, see p. 425, where dispersal and phylogeny are discussed).

Scott (1966: 253), discussing the subfamilial classification of the family, suggested that "a more natural division of the family would appear to involve the association on one hand of forms with more than 50 vertebrae and on the other hand of forms with fewer than 50 vertebrae." *G. gracilis* McDowall from New Zealand has 47–50 vertebrae, the lowest number recorded for the family in New Zealand. This species is almost certainly derived from *G. maculatus* (Jenyns), which has 59–64 vertebrae, the maximum for the family in New Zealand. Thus, in this simple case of landlocked speciation, *G. gracilis* has traversed the full range of vertebral number for *Galaxias* in New Zealand. According to Scott's proposal, it has thus moved from one subfamily to the other. Bearing in mind the effect of temperature on verte-

bral number, it is clear that this is not a useful character at the subfamilial, or even generic level. Scott (1966) also made use of pelvic fin ray number, combining species that exhibit reduction in the number of rays from the usual seven. I do not think that this is a useful character either. Within the New Zealand Galaxiidae alone, reduction in pelvic fin ray number has almost certainly taken place in three widely divergent lines—those leading to *N. burrowsius* (Phillipps), *G. divergens* Stokell, and *G. usitatus* McDowall. I think there is a need for the generic classification of the family to be based on more fundamental characters than vertebral and pelvic fin ray number, and for the classification to better express natural groupings and phylogeny. For these reasons, only two genera are recognized for the New Zealand Galaxiidae in the present study—*Galaxias* Cuvier and *Neochanna* Günther, following Stokell (1945, 1949).

Key to Genera

Mesopterygoidal teeth, epipleural ribs, supraethmoid and ventral ethmoid present, pelvic fins six or more rays . . . . . *Galaxias*

Mesopterygoidal teeth reduced or absent, epipleural ribs, supraethmoid and ventral ethmoid absent, pelvic fins five or fewer rays, or fins and girdle absent. . . . . *Neochanna*

GALAXIAS CUVIER

Galaxias Cuvier, 1817: 183 (type species *Galaxias fasciatus* Gray by subsequent monotypy).

Mesites Jenyns, 1842: 118 (type species *Mesites attenuatus* Jenyns 1842 by subsequent designation, Jordan, 1919: 212, preoccupied by *Mesites* Schoennherr, 1838, Coleoptera).

Austrocobitis Ogilby, 1899: 158 (type species *Mesites attenuatus* Jenyns, 1842 by subsequent designation, Whitley, 1956a: 34).

Diagnosis. Trunk cylindrical to a little compressed, naked; dorsal fin origin very posterior, about above vent. Pelvic fins present, six to eight rays, commonly seven; pectoral fin positioned laterally to low lateroventrally. Caudal fin usually with 16 principal rays, sometimes reduced to 15 or fewer. Jaw teeth conical, uniserial, with or without canines; mesopterygoidal teeth well developed to rudimentary, uniserial; lingual teeth biserial. Median supraethmoid and ventral ethmoid present; postcleithrum present or absent; epipleural ribs present.

Key to Species of *Galaxias*

This key is adapted from McDowall (1966b), incorporating taxonomic changes made since that time and those proposed in the following pages.

1. Lower jaw much longer than upper ..... *G. prognathus*, p. 393.
   Lower jaw not much longer than upper .. 2.
2. Lower jaw much shorter than upper, tucks behind upper when mouth closed 3.
   Jaws sub-equal, lower if shorter not tucking behind upper ..... 4.
3. Canine teeth strongly developed ..... *G. brevipinnis* p. 363.
   Canine teeth lacking ..... *G. postvectis* p. 361.
4. Pyloric caeca long, length much greater than breadth ..... 5.
   Pyloric caeca short to absent, usually short stubs ..... 6.
5. Vertebrae 49–57, gill rakers 9–13, depth of caudal peduncle usually much less than length ..... *G. vulgaris* p. 372.
   Vertebrae 58–61, gill rakers 14–17, depth of caudal peduncle sub-equal to length ..... *G. argenteus* p. 352.
6. Canines well developed .. *G. fasciatus* p. 355.
   Canines lacking or weak ..... 7.
7. Gill rakers very short, 11 or fewer ..... 8.
   Gill rakers long, 11 or more ..... 9.
8. Usually six pelvic rays, 15 caudal rays ..... *G. divergens* p. 384.
   Usually seven pelvic rays, 16 caudal rays ..... *G. paucispondylus* p. 390.
9. Gill rakers up to 17, vertebrae 54 or more ..... 10.
   Gill rakers 18–23, vertebrae 47–50 ..... *G. gracilis* p. 384.
10. S.L./H.L. 22.0–24.6%, 54–59 vertebrae ..... *G. usitatus*, p. 382.
    S.L./H.L. 18.5–21.6%, 59–64 vertebrae ..... *G. maculatus* p. 378.

Galaxias argenteus (Gmelin, 1789) Figure 4

Esox argenteus Gmelin, 1789: 1393 (holotype: unknown; locality: a small lake in Dusky Bay (Dusky Sound?), New Zealand.)

Esox alepidotus Bloch and Schneider, 1801: 395 (replacement name for *E. argenteus* Gmelin, 1789): Cuvier, 1817: 184; Forster, 1844: 142.

Galaxias alepidotus: Richardson, 1843: 25; Dieffenbach, 1843: 219; Richardson, 1848: 77; Günther, 1866: 208; Hutton, 1872: 58; 1889:

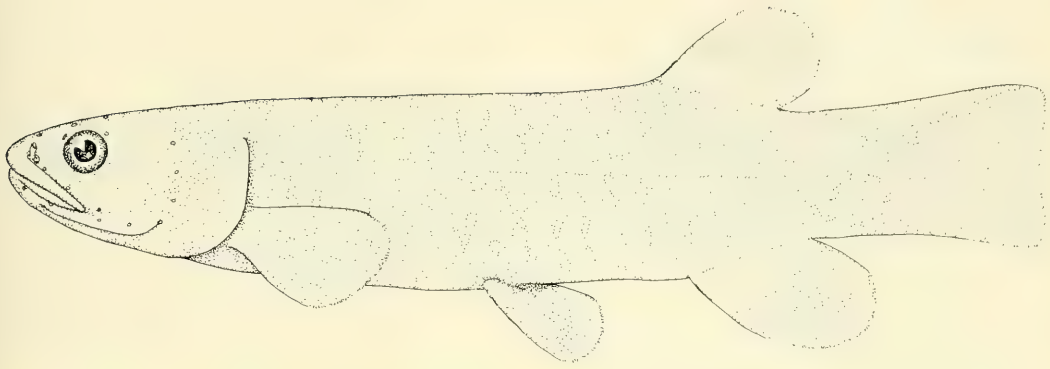

Figure 4. *Galaxias argenteus* (Gmelin), 280 mm L.C.F., Little Waitangi Stream, Pauatahanui Inlet.

284; 1896: 317; 1904: 51; Regan, 1905: 375; Waite, 1907: 12; Phillipps, 1927a: 13; Stokell, 1949: 493; 1954: 419.

Galaxias forsteri Valenciennes, *In* Cuvier and Valenciennes, 1846: 531 (replacement name for *Esox alepidotus* Bloch and Schneider, 1801).

Galaxias grandis Haast, 1872: 278 (holotype: apparently lost, see Stokell, 1949: 493; locality: creeks near Lake Ellesmere); Hutton, 1874: 107; 1904: 51.

Galaxias kokopu Clarke, 1899: 88 (holotype: unknown; locality: western slopes, South Island); Hutton, 1904: 51.

Galaxias argenteus: Whitley and Phillipps, 1940: 230 (partim); Stokell, 1960: 235.

Diagnosis. Differs from *G. fasciatus* Gray (Fig. 6) in coloration and in having very strongly developed pyloric caeca, longer head, more posterior pelvic insertion, higher depth of caudal peduncle/length of caudal peduncle ratio and jaw in head ratio (i.e., longer jaws), eye further forward in head and somewhat higher pectoral fin ray counts. Overlap in most of these characters is considerable and coloration is the most useful character. *G. argenteus* has numerous, small, irregular, gold spots on the dark trunk, while *G. fasciatus* has more regular vertical pale bands.

Differs from *G. postvectis* Clarke (Fig. 9) in coloration, in having stronger development of canine teeth in the jaws, much longer head and jaws, the jaws subequal, the eye further forward in the head, longer anal fin base, more posterior pelvic fin insertion, more anal fin rays, and somewhat higher numbers of branchiostegals and gill rakers. Coloration is again the most useful means of differentiating these species, jaw length, especially the shortened lower jaw in *G. postvectis* also enabling easy separation.

Description. Stout bodied, trunk somewhat rectangular in section and flattened dorsally, mid-dorsal groove moderately to well developed. Trunk deep, deeper than broad, greatest depth at or in front of pelvic fins. Depressed dorsally on head, considerably compressed posteriorly on caudal peduncle which is very short and deep, usually deeper than long. Lateral line an indistinct lateral furrow; accessory lateral line present but difficult to distinguish. Head very long, a little broader than deep. Eye moderately large and set moderately deep on lateral head, eye diameter/head length ratio not high because of great length of head; interorbital convex, very broad; jaws about equal, prominent. Lips thick and fleshy; cleft of mouth moderately oblique, reaching to between middle and posterior margin of eye. Profile of lower jaw from ventral aspect deep and rather narrow, U-shaped. Canine teeth well developed laterally in both jaws; mesopterygoidal teeth strongly developed; gill rakers long; pyloric caeca strongly developed.

Unpaired fins well developed, with thick fleshy bases; dorsal base of moderate

length, anal base long; both fins have greatest fin length much exceeding basal length, with rounded distal margins. Dorsal fin set well back, anal origin below or a little behind dorsal origin. Pectoral fins moderately long but not expansive, fleshy, inserted moderately low lateroventrally. Pelvic fins very long, expansive, and fleshy. Caudal fin long, thick and fleshy, depth noticeably less than body depth; truncated or a little emarginate in small specimens; caudal peduncle flanges well developed, extending forward almost to anal fin insertion.

Variation. Meristic: dorsal 10 (16), 11 (21), 12 (2); caudal 15 (1), 16 (38); anal 12 (13); 13 (20), 14 (5), 15 (1); pelvic 7 (38), 8 (1); pectoral 13 (7), 14 (27), 15 (5); branchiostegals 7 (2), 8 (33), 9 (4); vertebrae 58 (4), 59 (16), 60 (15), 61 (2); gill rakers 4–10 (3), 4–11 (7), 4–12 (1), 5–10 (4), 5–11 (21), 5–12 (2). Morphometric: see Table 1, p. 358.

Coloration. Often dark, a deep gray-brown, sometimes paler, approaching a buff color. The head, dorsal and lateral trunk, and fin bases are profusely covered with delicate, gold spots, lines, crescents and rings. These tend to be finer dorsally and on the head, coarser and bolder on the trunk. The belly is usually paler, bluish gray in dark examples, correspondingly lighter in paler specimens. A bluish blotch is present above and behind the pectoral fin base, but in heavily pigmented fishes it is of similar color to the trunk and is indistinct.

Size. Clarke (1899: 83) reported that *G. kokopu* (= *G. argenteus*) grows to 23 inches (584 mm) and a weight of six pounds. Haast (1872: 278) recorded a specimen 19.3 inches (490 mm) and Stokell (1949: 494) one of 17 inches (432 mm). *G. argenteus* is thus reliably reported to grow to much greater size than any other galaxiid, although large examples are now very rare. The largest specimen I have seen was 330 mm and others were commonly up to about 280 mm long.

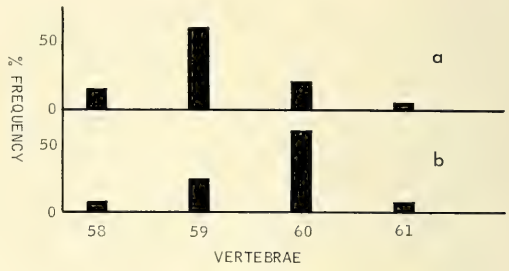

Figure 5. Variation in vertebral number in *Galaxias argenteus*. A, Localities in the southwest of the North Island —Wellington District (20 examples); B, Localities in the west of the South Island (17 examples).

Population differences. There was little scope amongst the few specimens examined for revealing regional variation in *G. argenteus*. From grouping samples from the Wellington Province, and those from the west coast of the South Island, there appears to be slight displacement in dorsal fin ray number, the northern examples having modally fewer rays than those from the south. A similar displacement in vertebral number is evident (Fig. 5). These differences are slight, but further study of more adequate samples may confirm the southward increase in meristics hinted at here.

Habitat. G. argenteus is exclusively lowland in range, inhabiting pools in lowland swamps and streams. It is an uncommonly seen species, usually lurking beneath cover, and is probably nocturnal, feeding in more open water during the night. Haast (1872: 278) reported catching *G. argenteus* of large size from very small streams, and such waters appear to be a characteristic habitat, especially when overgrown with flax (*Phormium tenax*) and raupo (*Typha angustifolia*). Collections from the west coast of the South Island have shown that *G. argenteus* is sometimes common in flax swamps and also occurs in the bush-stained, tea-colored streams there. It has also been taken from Lake Brunner (G. A. Eldon, pers. comm.) and may be more common in shallow weedy lakes than present records indicate.

Life history. Specimens of *G. argenteus* collected in March included a female approaching maturity and a ripe male. Others collected during September to December had very immature gonads. These data suggest autumn or early winter spawning. *G. argenteus* has a whitebait juvenile comparable with juveniles of *G. fasciatus* and *G. postvectis*, which migrates into fresh water during the spring. These species with whitebait juveniles migrate upstream together, and this suggests that they may spawn at about the same time, during the autumn or early winter.

Nothing is known of the spawning locality, although spawning migrations are not suspected. The eggs of the female approaching maturity were too small for useful size determination, but this fish, 251 mm long, contained about 11,000 eggs.

After hatching, the larvae are probably carried downstream to the sea, where larval and juvenile development occurs. At their subsequent upstream migration, the whitebait of *G. argenteus* are transparent, with very little pigmentation (Fig. 43) and are comparatively large (50–55 mm). Soon after migration, trunk pigmentation increases and intensifies to a dark gray-brown, eight to ten pale blotches or bands develop across the lateral trunk, and the adult pattern finally becomes superimposed on the juvenile banding. The stout, deep-bodied form of the adult is rapidly attained.

Distribution. G. argenteus is widely distributed in lowland localities that are accessible from the sea. It is known from the following: Mokau River (Fig. 7: 25); Pokaka Stream (27); Waikawa Stream (32*); Waikanae River (36*); Whareroa Stream (39*); Horokiri Stream (40); Little Waitangi Stream (41*); Trotter's Gully Stream (44) and Hawkin's Gully Stream Stream (45*), Makara System; Belmont Stream (48) and Moonshine Stream (42), Hutt System; York Bay Stream (51*); Day's Bay Stream (53); Wainuiomata River (50); Wairarapa (55, Stokell, 1949: 494); tributaries of Lake Ellesmere (89, Haast, 1872: 278); Mokihinui River (69); Buller River (71); Grey River (72); Lake Haupiri (73); Lake Brunner (74*); Lake Kaniere (77); Lake Ianthe (79*); Whataroa River (80*); Lake Paringa (81, Haast, 1872: 278); Moeraki River (82); Dusky Bay (86, Dusky Sound?, type locality, Forster, 1778: 159); Stillwater River (87); Milford Sound (85, Hutton, 1896: 317); Southland (91, Stokell, 1949: 494); Horseshoe Bay Creek (93); Chatham Islands (94, Skrzynski, 1967: 95).

* From P. 345.

Galaxias fasciatus Gray, 1842
Figure 6

Galaxias fasciatus Gray, 1842: 73 (syntypes (3): BMNH 1967.8.14.9–11, not seen; locality: River Thames, New Zealand); Dieffenbach, 1843: 221; Valenciennes, *In* Cuvier and Valenciennes, 1846: 350; Richardson, 1843: 25, 1848: 77; Günther, 1866: 209; Kner, 1865: 319; Hutton, 1872: 59; Clarke, 1899: 90; Hutton, 1904: 51; Regan, 1905: 374 (partim); Phillipps, 1926b: 293, 1927a: 13, 1940: 15; Stokell, 1949: 492.

Galaxias reticulatus Richardson, 1848: 76 (syntypes (3): BMNH 1967.8.14.12–14, not seen; locality: Auckland Islands?).

Galaxias brocchus Richardson, 1848: 76 (holotype: BMNH 1855.9.19.800, not seen; locality: Auckland Islands?).

Galaxias argenteus: Whitley and Phillipps, 1940: 230 (partim).

Diagnosis. Differs from *G. argenteus* (Gmelin) (Fig. 4) in characters discussed in the diagnosis of that species (p. 353); differs from *G. postvectis* Clarke (Fig. 9) in coloration, in the absence of pyloric caeca and the presence of better-developed canine teeth in the jaws, in its longer and more slender head, and in its longer jaws, particularly the lower jaw. *G. postvectis* has somewhat fewer anal fin rays and branchiostegals, and more vertebrae and gill rakers.

Taxonomy. Two names that Stokell (1949) failed to apply to any New Zealand galaxiids are *G. brocchus* Richardson and *G. reticulatus* Richardson, described from

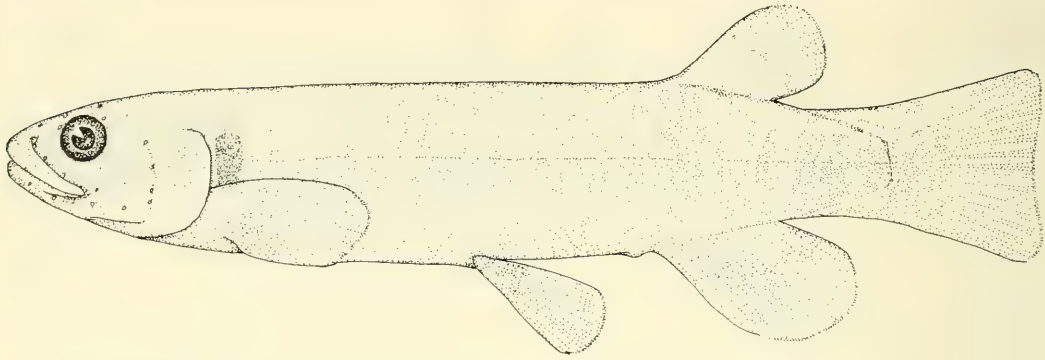

Figure 6. *Galaxias fasciatus* Gray, 155 mm L.C.F., Makahika Stream, Ohau River System.

the Auckland Islands. They were treated as synonyms of *G. fasciatus* by both Günther (1866: 209) and Regan (1905: 374). Fishes of this type have not otherwise been recorded from the sub-Antarctic islands of New Zealand, the only species there being *G. brevipinnis* Günther. Both Günther and Regan based their identifications on re-examination of Richardson's material, and the excellent likenesses of *G. fasciatus* in Richardson's figures (his plates 42 and 43) definitely support the view of Günther and Regan. Despite several collections from these islands (e.g., the Cape Expedition, 1941–45, see Stokell, 1950), *G. fasciatus* has not been re-collected there, and there is no evidence to suggest it is present. It is possible that it has become extinct in the islands since Richardson's fishes were collected, or that the material he studied was incorrectly labeled. Since *G. fasciatus* has marine larvae and juveniles, its dispersal to the sub-Antarctic islands is comprehensible, although its temperature preferences appear to be higher than those of *G. brevipinnis* (McDowall, 1965a: 299), indicating that these islands are probably less suited to *G. fasciatus* than to *G. brevipinnis*, which is present there. The possibility that the specimens were incorrectly labeled remains nothing more than a possibility. Nevertheless, *G. brocchus* and *G. reticulatus* are probably best regarded as synonyms of *G. fasciatus*, and as not occurring on the sub-Antarctic islands of New Zealand, until further collections indicate otherwise.

Description. Stout bodied, trunk squarish to rounded in section, somewhat flattened dorsally with middorsal furrow present; trunk deep, greatest body depth at or a little in front of pelvic fins, depressed anteriorly on head and much compressed on caudal peduncle, which is short and about as deep as long. Lateral line a distinct lateral groove; accessory lateral line present. Head prominent, broader than deep and somewhat depressed; eye large, towards upper head profile, interorbital convex, very broad. Jaws about equal, lips prominent; cleft of mouth reaching beyond middle of eye, oblique. Profile of lower jaw from ventral aspect deep and narrow, U-shaped. Canine teeth strongly developed laterally in both jaws, mesopterygoidal teeth well developed; gill rakers well developed; pyloric caeca lacking.

Median fins well developed, with thick fleshy bases; prominent, greatest fin length much greater than base length, distal margin of fin much rounded; anal origin about below dorsal origin. Pectoral fin prominent and fleshy, rounded in outline; insertion moderately low. Pelvic fin expansive and long, inserted behind mid-point of standard length. Caudal fin fleshy, long, emarginate or truncated, emargination usually becom-

Figure 7. Distribution of *Galaxias argenteus*, *G. fasciatus*, and *G. postvectis* (numbers in figure as in text pp. 355, 360, and 363).

TABLE 1. MORPHOMETRIC VARIATION IN LARGE, STOUT-BODIED SPECIES (FIGURES GIVEN AS PERCENTAGES OF DENOMINATOR OF RATIO).

	G. argenteus			*G. fasciatus*			*G. postvectis*		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	83.3	85.5	87.0	82.6	85.5	87.7	84.0	87.0	88.5
B.D.V./S.L.	18.7	21.0	23.4	15.0	17.9	21.4	16.4	19.6	22.4
L.C.P./S.L.	9.8	11.4	13.5	10.8	12.0	14.9	12.1	13.2	14.4
D.C.P./L.C.P.	100.0	113.6	125.0	61.0	76.9	114.9	95.2	102.0	113.6
Pre D./S.L.	74.6	76.3	77.5	73.0	76.5	79.4	70.9	74.1	76.9
Pre D./Pre A.	94.3	98.0	102.0	96.2	100.0	102.0	92.6	97.1	100.0
D.F.B./S.L.	9.4	11.9	13.4	9.5	10.8	11.9	10.2	11.3	11.6
D.F.B./D.F.M.	45.7	55.6	68.5	47.6	54.6	64.1	50.0	58.1	65.4
A.F.B./S.L.	13.5	15.4	17.8	11.9	14.0	16.1	11.1	13.4	14.4
A.F.B./A.F.M.	55.3	61.7	76.3	54.4	61.4	70.4	53.8	61.7	66.2
Pre Pel./S.L.	53.5	56.4	58.1	48.8	53.2	56.8	50.3	52.9	56.2
Pec.Pel./S.L.	26.8	29.1	31.3	26.8	29.4	32.7	28.9	31.8	35.3
Pec./Pec.Pel.	48.2	60.7	68.5	50.6	60.5	72.4	41.3	53.1	67.3
Pel.An./S.L.	20.8	22.7	25.0	21.4	24.1	27.4	23.1	24.8	26.5
Pel./Pel.An.	56.8	68.5	77.8	58.5	69.2	81.0	53.7	61.7	71.0
H.L./S.L.	27.0	29.1	30.5	22.8	25.9	28.6	21.2	23.0	25.0
H.D./H.L.	50.0	54.6	61.0	46.1	53.5	60.2	56.2	64.1	72.5
H.W./H.L.	57.5	64.9	74.1	55.9	71.4	78.1	59.5	70.4	78.1
Sn.L./H.L.	26.6	29.6	32.4	28.2	31.8	35.0	31.3	33.6	37.2
P.O.H.L./H.L.	50.8	55.6	61.4	45.7	50.5	55.0	49.0	50.8	54.1
Io.W./H.L.	40.0	42.5	46.1	40.3	43.9	47.4	40.5	44.8	47.4
D.E./H.L.	14.8	17.7	22.2	16.7	20.2	24.5	17.8	19.9	23.5
L.U.J./H.L.	41.2	43.7	45.7	42.4	48.5	51.8	37.5	40.7	43.3
L.M./H.L.	37.7	41.3	43.9	40.8	45.5	50.0	27.5	33.0	35.7
W.G./H.L.	33.7	37.3	42.4	33.3	40.8	46.5	34.4	38.8	42.6
Fish examined		36			60			25	

ing reduced with growth; fin depth usually somewhat less than greatest body depth; caudal peduncle showing considerable development of flanges.

Variation. Meristic: dorsal 9 (15), 10 (47), 11 (13), 12 (2), 13 (2); caudal 15 (1), 16 (60), 17 (2); anal 11 (3), 12 (29), 13 (42), 14 (10), 15 (1); pelvic 7 (63); pectoral 12 (20), 13 (47), 14 (7), 15 (4); branchiostegals 6 (3), 7 (18), 8 (40), 9 (3); vertebrae 56 (1), 57 (11), 58 (22), 59 (26), 60 (2), 61 (1); gill rakers 4–8 (1), 4–9 (5), 4–10 (3), 4–11 (3), 5–9 (5), 5–10 (19), 5–11 (1), 5–12 (1). Morphometric: see Table 1.

Coloration. Trunk color a dark purplish gray, banded dorsally and laterally with a series of narrow, pale, vertical bands. The bands are numerous in young fish, becoming narrower and more restricted to the posterior of the trunk as the fish grow. Lateroventrally, the trunk coloration alters quite abruptly to a dull purplish brown. There is a prominent, dark, blue-black blotch above and behind the pectoral fin base. Frequently living in small, bush-covered creeks and streams, *G. fasciatus* appears well adapted to broken lighting conditions.

Size. G. fasciatus is one of the largest species of *Galaxias* and is known to grow to 260 mm. It commonly reaches 200 mm.

Population differences. Regional character differences were not found in diadromous populations of *G. fasciatus* from widely separated localities, although more intensive studies may show that they do occur.

Taxonomically interesting differences between diadromous and lacustrine populations were found. The fishes from Lake Okataina and the Kaihoka Lakes were

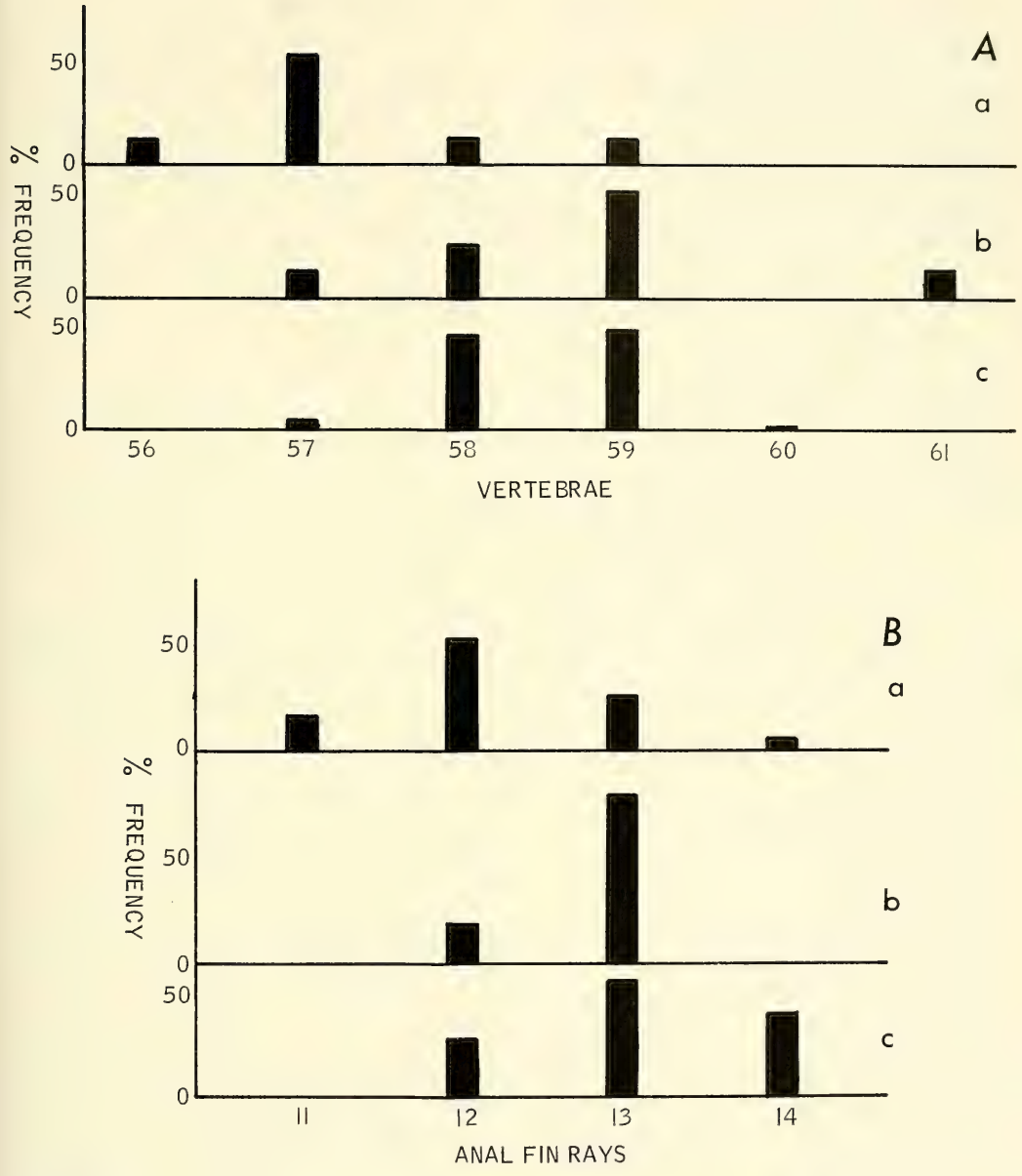

Figure 8. Variation in meristics in *Galaxias fasciatus*. A, Vertebrae; B, Anal fin rays; a, Lake Okataina (8 examples); b, Kaihoka Lakes (8 examples); c, Diadromous populations (47 examples).

found to be considerably more slender than sea-going fishes, and those in the Kaihoka Lakes had a shorter head (mean H.L./S.L. 25.9 in diadromous and 24.3 in Kaihoka populations). Lake Okataina examples had fewer vertebrae and fewer rays in the anal fin (Fig. 8), although overlap with diadromous fishes was substantial. Fewer branchiostegals were present in the fishes from the Kaihoka Lakes.

again with overlap (mean number, Kaihoka 6.75, diadromous 7.83).

As such landlocked populations become better understood, it may become necessary to recognize them as separate taxa at the species or subspecies level, as has been done with *G. maculatus*, but existing data do not justify this.

Habitat. G. fasciatus is essentially a lowland species, although it shows moderate penetration of river systems, even where substantial falls are present. Adults have been collected from small pools on the faces of high waterfalls and the juveniles are known to be able to climb wet, smooth surfaces with ease and rapidity. The locality furthest from the sea where *G. fasciatus* is known is the Kahuterawa Stream, a tributary of the Manawatu River about 40 miles upstream from the sea (C. L. Hopkins, pers. comm.). *G. fasciatus* is found mostly in small, quiet, winding creeks in coastal and lowland bush, usually hiding beneath cover such as logs, overhanging banks, tree roots etc., or amongst rock aggregations at the bases of small pools and cascades in the streams. This species is also quite common in the tannin-stained waters of flax swamps on the west coast of the South Island. Sea-going populations occur in Lakes Ianthe and Mapourika, in addition to the previously mentioned landlocked populations.

Life history. The breeding site of *G. fasciatus* is undescribed, but since ripe adults were collected in typical adult habitat, it seems unlikely that there is an adult breeding migration. Ripe males were collected with milt running as early as the end of February and study of gonad maturity suggests that breeding takes place mostly during the autumn and early winter (February to May or June). The eggs are of moderate size, 1.3–1.6 mm in diameter, and numerous; a female 160 mm long contained 5,100 eggs. The larvae are apparently carried to sea after hatching, and a subsequent upstream migration of the juveniles occurs the following spring, together with the whitebait of other diadromous species, although relatively late in the overall migration period (McDowall, 1965a). At migration the young *G. fasciatus* are transparent, little pigmented (Fig. 41), and measure 38–48 mm. Trunk pigmentation develops quickly after the fish enter fresh water, beginning as a general covering of melanophores; later a series of narrow, alternating light and dark bands develops. The slender juveniles become much stouter and the banding bolder, as the number of bands along the trunk increases. Eventually they extend over the dorsum of the trunk, where they form a reticulum of lighter markings on the more intense trunk coloration. With increasing size, the banding decreases in boldness and finally becomes obliterated along the anterior two-thirds of the trunk, especially in very large adults.

Distribution. The range of *G. fasciatus* is very extensive, especially on the western coasts of New Zealand. It is known from the following localities: Awanui River (Fig. 7: 1); Cavalli Islands (2); Kerikeri River (3); Mangamuka Stream (4*); Wainui River, tributary of the Orouaiti River (5); a stream at Waiomio (6); Merowhanara Stream, Waipoua System (7*); tributary of the Wairoa River at Tangaihi (8); tributaries of the Hakaru River at Mangawai (9); Chicken Islands (10, Stokell, 1949: 493); Little Barrier Island (11); Makarau River (12); a stream at Atkinson's Park, Titirangi (13); Whangamarino Stream (14); Mauku Stream (15); Waihou River (16, ? = Thames River, type locality); tributary of Kauaeranga River (17); Tairua River (18*); Waimai Stream (19); Pikowai Stream (20); Whakatane River (21); Lake Okataina (23*); Whanarua Stream (24*); Mokau River (25); Rangitikei River (28); Manawatu River (29); Kahuterawa Stream (30); Makahika Stream, Ohau System (31*); tributary of Otaki River at Otaki Forks (33*); Mangaone Stream, Te Horo (34); Waikanae River (36); Whareroa Stream (38*); Horo-

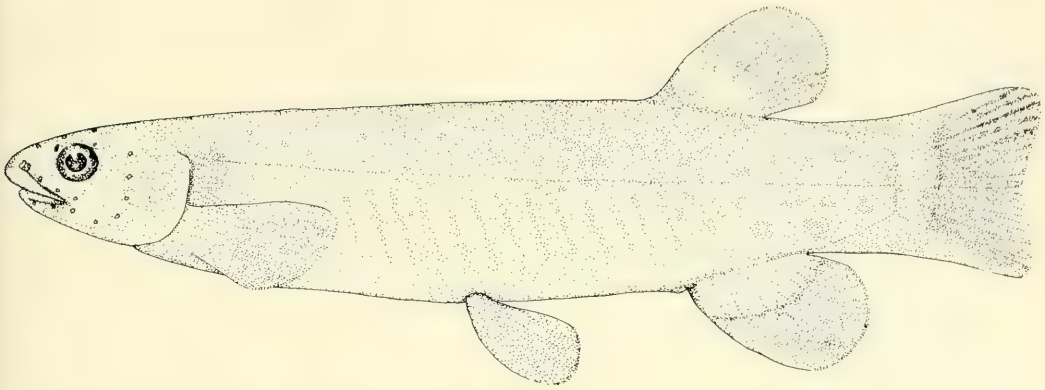

Figure 9. *Galaxias postvectis* Clarke, 178 mm L.C.F., stream at Otaki Forks, Otaki River System.

kiri Stream (40); Little Waitangi Stream (41); Tawa Stream (43); Makara Stream (45*), Hawkin's Gully Stream, a Makara tributary (44*); Kaiwharawhara Stream (46); Hutt River (49); Catchpool Stream, Wainuiomata System (50); Day's Bay Stream (53*); tributary of Lake Onoke (54); Whangamoana Stream (56*); Kapiti Island (57); Ngarururoro River (58); Pongoroa River (59); Arapawa Island (60); D'Urville Island (61); Momorangi Bay Stream (63*); Wairau River (64); "Nelson" (65, Stokell, 1949: 493); Kaihoka Lakes (66*); Karamea River (67); Little Wanganui River (68); Ngakawau River (70); Buller River (71); Grey River (72); Hokitika River (75); Taramakau River (76); Lake Ianthe (77*); Wanganui River (78); Lake Mapourika and Whataroa River (80*); Lake Paringa (81); Moeraki River (82); Jackson Bay Stream (83*); Awarua River (84); Waitati River (90*); Banks Peninsula (88); Stewart Island (92, Stokell, 1949: 493); Chatham Islands (94, Skrzynski, 1967: 95).

These localities show that *G. fasciatus* occurs commonly in western areas, and in the east in the North Auckland—Bay of Plenty districts. The general absence of the species from the east coast is probably the result of a combination of little suitable habitat and the fewer collections made, especially along the east coast of the North Island. No localities are known to me from Southland and this is probably also due to the lack of collection.

Galaxias postvectis Clarke, 1899
Figure 9

Galaxias postvectis Clarke, 1899: 88 (holotype: unknown; locality: "western slopes," South Island); Stokell, 1960: 237.
Galaxias fasciatus: Regan, 1905: 374 (partim).
Galaxias charlottae Whitley and Phillipps, 1940: 230 (holotype: DMNZ 981, seen; locality: Queen Charlotte Sound).
Galaxias argenteus: Whitley and Phillipps, 1940: 231 (partim).

Diagnosis: G. postvectis differs from *G. argenteus* (Gmelin) (Fig. 4) and *G. fasciatus* Gray (Fig. 6) in characters noted in the diagnoses of these species (pp. 353 and 355 respectively).

Description. Stout bodied, trunk rounded in section, not flattened dorsally, with no middorsal groove, rather turgid-looking. Trunk deeper than broad, depressed anteriorly on head, which is not much flattened dorsally, compressed on caudal peduncle, which is short and deep, depth about equal to length. Lateral line an indistinct midlateral furrow; accessory lateral line present. Head prominent, a little broader than deep. Eye large, moderately deep set, interorbital convex, very broad. Jaws well developed, lower much shorter than upper, cleft reaching to about anterior

third of eye, oblique. Profile of lower jaw from ventral aspect rather deep and narrow, U-shaped. Canine teeth poorly developed in jaws, or lacking; mesopterygoidal teeth moderately developed; gill rakers and pyloric caeca moderately long.

Unpaired fins well developed with thick, fleshy bases, greatest fin length much greater than basal length; anal origin a little behind dorsal origin. Pectoral fin well developed, inserted moderately high, somewhat triangular in shape, with longest rays near upper margin. Pelvic fins long and expansive, inserted behind midpoint of standard length. Caudal fin rather fleshy, moderately long, emarginate, tending towards truncation in very large individuals, fin depth a little less than greatest body depth; caudal peduncle flanges well developed.

Variation. Meristic: dorsal 9 (6), 10 (15), 11 (4); caudal 16 (25); anal 10 (1), 11 (10), 12 (14); pelvic 7 (25); pectoral 13 (2), 14 (14), 15 (9); branchiostegals 6 (2), 7 (21), 8 (2); vertebrae 59 (5), 60 (8), 61 (8), 62 (1); gill rakers 4–12 (1), 5–11 (3), 5–12 (1), 5–13 (2), 6–11 (10), 6–12 (5), 6–13 (2), 7–12 (1). Morphometric: see Table 1, p. 358.

Coloration. Usual body color a deep brownish blue, with paler, indistinct, irregular marbling of slightly darker shade on the dorsal and dorsolateral trunk, and extending on to the lateral and lateroventral trunk or resolving into faint, slightly oblique bands. A purplish blotch is present above the pectoral fin base. Ventrally, the trunk is paler, more brownish in color, but nevertheless intensely pigmented. In transmitted light the fin bases appear a rufous color. Between the fin rays on the distal two-thirds to half of the median fins, there is bold and distinctive brown-black banding, which fades as the fleshiness of the fin bases develops.

Size. The largest individual examined measured 250 mm, but Stokell (1960: 238) listed one at 261 mm. Individuals 180–200 mm long were relatively abundant.

Population differences. Insufficient large samples were available to enable meaningful comparison of samples from different localities.

Habitat. G. postvectis is almost always collected from small, heavily bush-covered streams that are unmodified by agricultural development. These streams are usually stable, with small pools, often overhung with tree roots, or containing fallen trees. Logs in the streams often form small pools and cascades, and *G. postvectis* occurs in these. It is probably very sensitive to removal of bush cover and stream modification.

Life history. The life history pattern of *G. postvectis* is similar to that of the other stout-bodied species. The eggs appear to be relatively small, although the only ripe individuals examined were somewhat dehydrated, preventing satisfactory measurement of the eggs. In these fishes, the eggs were 1.0–1.5 mm diameter. A female 205 mm long contained about 13,000 eggs. The breeding site is undiscovered, but is likely to be close to the normal adult habitat. The larvae are apparently carried downstream to the sea, and develop and grow in the sea during the winter. The upstream migration of the whitebait juveniles occurs concurrently with the other species, although probably towards the end of the migration period, along with *G. fasciatus* and *G. argenteus.* Adults collected from the Ohau River system in February showed gonads to be at an early stage of maturation; one fish from the Mangaone Stream, taken in late May, and another from the Waikanae River in early June had ova about ripe. Further examples collected from the Waikanae River in early September were spent or in early stages of gonad rejuvenation. Thus spawning probably occurs in autumn or early winter.

The transparent whitebait of *G. postvectis* (Fig. 44) develop a covering of melanophores soon after entering fresh water, but do not develop pale bands like the young of *G. fasciatus* and *G. argenteus.*

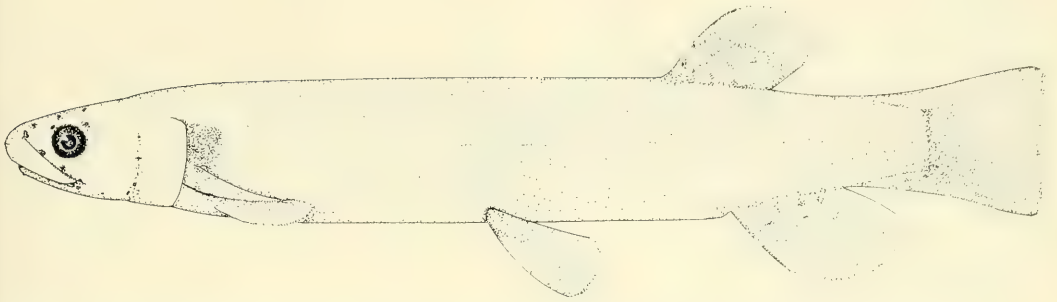

Figure 10. *Galaxias brevipinnis* Günther, 185 mm L.C.F., stream at Erua, Upper Wanganui River System.

Dusky brown bands develop along the sides of the trunk as the fishes grow and attain the stout-bodied form of the adult.

Distribution. Like the other species with marine juveniles, *G. postvectis* is rather widely distributed in New Zealand. Collection localities are few, even though they extend along the west coast of New Zealand from the Waipoua Kauri forests in North Auckland to the Awarua River, Big Bay, in the south. Localities in the Bay of Plenty and the Marlborough Sounds are also known. As yet, *G. postvectis* has not been recorded from the east coast between East Cape and Southland. This probably represents a real distributional gap for much of the Canterbury area, but *G. postvectis* seems likely to be found in some Southland streams and on Banks Peninsula, where overgrown bush streams with stable, rocky beds are present. Very little collection has been done on the east coast of the North Island, and *G. postvectis* may also be found to occur there. It is presently known from the following localities: Merowhanara Stream (Fig. 7: 7*); Waimana River (22); Ratapiko (26); Kahuterawa Stream, Manawatu System (30); Makahika Stream, Ohau System (31*); a stream at Otaki Forks, Otaki River (33*); Waikanae River and its tributaries, the Mangakotukutuku (35*) and Ngatiawa Streams (37*); Whareroa Stream (38); Little Waitangi Stream (42); Day's Bay Stream (53); Owhiro Bay Stream (47*); Queen Charlotte Sound (62, Whitley and Phillipps, 1940: 230); Mokihinui River (69); Buller River (71); Waimea River (76*); Awarua River (84).

Galaxias brevipinnis Günther, 1866
Figure 10

Galaxias brevipinnis Günther, 1866: 213 (syntypes (3): BMNH 1853.2.14.5–7, not seen; locality: New Zealand); Hutton, 1872: 59, 1896: 317, 1904: 51; Regan, 1905: 374; Waite, 1909: 586; Rendahl, 1926: 2; Phillipps 1927a: 13, 1940: 21; Stokell, 1954: 415, 1960: 236.

Galaxias olidus: Hutton, 1872: 270 (not *G. olidus* Günther, 1866: 209).

Galaxias campbelli Sauvage, 1880: 229 (syntypes (4): MNHNP A-2381, not seen; locality: Campbell Island); Stokell, 1949: 487, 1950: 8.

Galaxias lynx Hutton, 1896: 317 (holotype: CMCNZ 70 seen, paratypes: CMCNZ 71 (3) seen, AMS IB-435–6 (2) not seen; locality: Lakes Coleridge and Wakatipu); Stokell, 1949: 486.

Galaxias robinsonii Clarke, 1899: 89 (holotype: unknown; locality: western slopes, South Island); Phillipps, 1926a: 98.

Galaxias bollansi Hutton, 1901: 198 (holotype: BMNH 1905.11.30.23, not seen; locality: Auckland Islands).

Galaxias huttoni Regan, 1905: 373 (syntypes (7): 1905.11.30.27–33, seen; locality: "Lake Rainiera," an unknown New Zealand place name); Phillipps, 1924b: 190.

Galaxias castlae Whitley and Phillipps, 1940: 229 (holotype: DMNZ 2070, seen; locality: Lake Waikaremoana).

Galaxias koaro Phillipps, 1940: 35 (holotype: unknown; locality: Lakes Rotoaira and Rotopounamu); Stokell, 1949: 487.

Diagnosis. Differs from *G. vulgaris* Stokell (Fig. 16) in having more vertebrae (especially in the south, where the two

species are sympatric) and somewhat higher fin ray counts in the dorsal, anal, and pectoral fins. The gill rakers are much better developed in *G. brevipinnis* than in *G. vulgaris*, and the lower jaw recedes further in the former species. *G. brevipinnis* breeds in the autumn and has migratory marine or lacustrine whitebait juveniles; in contrast, *G. vulgaris* breeds mostly in the spring and has no migratory juvenile.

Taxonomy. Nine nominal species of the *G. brevipinnis* type have been described. Stokell (1949: 486–490, 1954: 413, 1960: 236) reduced the number recognized to three, viz. *G. brevipinnis* Günther, *G. lynx* Hutton, and *G. koaro* Phillipps. Examination of many large samples from a great variety of localities has shown that these populations represent a single, variable species.

From the description of Regan (1905: 377), there appears to be little, if any, difference between *G. brevipinnis* and *G. weedoni* Johnston. In *G. weedoni*, Regan recorded canine teeth in the jaws, the cleft of the jaw extending below the eye, long, low-placed pectoral fins, a long, slender caudal peduncle, and a blue-black blotch above the pectoral fin base. Meristic data—vertebrae 57–60, dorsal fin rays 10–11, anal rays 10–12, pectoral rays 14–15, branchiostegals 8–9—are all consistent with the inclusion of *G. weedoni* in *G. brevipinnis*. I have seen only juveniles of *G. weedoni*, but their coloration is identical with that of juvenile *G. brevipinnis* and different from that of any other galaxiid I have seen. And they are long and slender, have a much shortened lower jaw, and have the anal fin set back below the middle of the dorsal, just as in *G. brevipinnis*. Accordingly, I think that the two species are conspecific, although formal synonymy of *G. weedoni* in *G. brevipinnis* must await examination of adult specimens.

Description. Elongate and slender-bodied, trunk rounded in section, somewhat flattened dorsally, with slight development of middorsal furrow; trunk much depressed anteriorly on head, compressed behind vent; dorsal and ventral trunk profiles about parallel. Caudal peduncle moderately long and slender, substantially longer than deep. Lateral line a somewhat indistinct lateral crease; accessory lateral line present. Head moderately long, much broader than deep, cheeks broadening below eye; jaws long, lower markedly shorter than upper and tucked behind it when mouth is closed, lips prominent. Snout short. Cleft of mouth slightly oblique, extending to about middle of eye, profile of lower jaw from ventral aspect deep and rather narrow, U-shaped, but gape broad in head length. Eye rather small, deep on lateral head, interorbital convex. Jaws with prominent canines laterally; mesopterygoidal teeth moderately well developed; gill rakers and pyloric caeca well developed.

Fins well developed, thick and fleshy; dorsal and anal short based but extending back well beyond bases, distal margins much rounded; anal origin usually well behind dorsal origin. Pectoral fin expansive, inserted low latero-ventrally, with lamina of fin directed ventrally; pelvic-anal interval rather short, fin expansive and long, inserted at about midpoint of standard length. Caudal fin truncated to slightly emarginate, fin tips somewhat rounded, depth about equal to body depth; peduncle flanges weakly to moderately developed.

Variation. Meristic: dorsal 9 (30), 10 (126), 11 (54), 12 (7); caudal 15 (5), 16 (206), 17 (3), 18 (1); anal 9 (3), 10 (21), 11 (113), 12 (61), 13 (18); pelvic 6 (4), 7 (201), 8 (12); pectoral 13 (4), 14 (50), 15 (113), 16 (48), 17 (2); branchiostegals 6 (1), 7 (54), 8 (125), 9 (36); vertebrae 52 (1), 53 (2), 54 (9), 55 (16), 56 (30), 57 (45), 58 (36), 59 (53), 60 (77), 61 (63), 62 (16), 63 (5), 64 (2); gill rakers 3–9 (4), 3–10 (5), 4–8 (2), 4–9 (67), 4–10 (53), 4–11 (9), 4–12 (1), 5–8 (1), 5–9 (4), 5–10 (13), 5–11 (6), 5–12 (1), 6–11 (1). Morphometric: see Table 2, p. 365.

Coloration. Usually dark colored, the

Table 2. Morphometric variation in large, slender species (figures given as percentages of denominator of ratio).

	G. brevipinnis			*G. vulgaris*		
	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	84.8	87.0	89.3	84.0	87.0	89.3
B.D.V./S.L.	11.0	13.2	15.3	11.0	12.9	15.4
L.C.P./S.L.	11.8	13.1	15.8	11.9	14.1	16.5
D.C.P./L.C.P.	59.5	71.9	88.5	56.2	69.4	94.3
Pre D./S.L.	68.5	73.5	81.3	67.6	71.9	75.8
Pre D./Pre A.	90.9	95.2	99.0	90.1	95.2	100.0
D.F.B./S.L.	7.8	9.4	10.8	7.2	8.9	10.7
D.F.B./D.F.M.	47.6	56.8	70.9	47.6	56.5	64.5
A.F.B./S.L.	8.8	10.5	12.2	8.9	10.5	13.4
A.F.B./A.F.M.	50.0	61.7	73.0	51.0	61.4	74.1
Pre Pel./S.L.	46.3	52.2	57.8	49.3	53.0	56.5
Pec.Pel./S.L.	27.2	30.7	36.8	28.2	32.0	36.4
Pec./Pec.Pel.	43.1	55.6	68.3	36.8	49.6	61.5
Pel.An./S.L.	20.9	25.7	30.4	19.6	23.1	26.5
Pel./Pel.An.	44.4	58.9	77.4	43.2	57.7	72.7
H.L./S.L.	20.7	23.6	28.7	20.5	23.4	27.0
H.D./H.L.	41.7	49.3	55.9	45.9	52.6	59.9
H.W./H.L.	56.2	67.6	78.7	57.5	67.1	78.1
Sn.L./H.L.	26.3	30.7	34.4	26.7	31.6	36.2
P.O.H.L./H.L.	48.5	55.0	70.4	43.7	51.8	58.1
Io.W./H.L.	32.5	37.7	44.1	34.5	38.6	43.7
D.E./H.L.	13.9	17.8	25.0	14.8	17.6	22.0
L.U.J./H.L.	37.3	42.9	48.1	33.3	43.1	51.0
L.M./H.L.	32.4	38.5	43.7	33.3	38.5	47.2
W.G./H.L.	40.0	42.7	56.2	35.1	43.5	55.6
Fish examined		160			215	

basic body color a dark gray-brown, the dorsal and lateral trunk covered with irregular greenish brown to gold vermiculations, sometimes as a coarse, bold reticulum or varying to dense, fine speckling. Belly paler, a smokey gray. A prominent blue-black blotch is present above and behind the pectoral fin base.

Size. *G. brevipinnis* is one of the larger Galaxiidae, the largest examined by the writer being 220 mm long. An example described by Phillipps (1926a: 99) as *G. robinsonii* Clarke was 9.6 inches (240 mm) and one described by Clarke (1899: 99) 8.2 inches (213 mm) long. *G. brevipinnis* commonly grows to 160–185 mm.

Population differences. Populations of fishes belonging to *G. brevipinnis* are widespread in lakes and rivers throughout New Zealand, and examination of populations from too few and too isolated localities, together with the variability between these populations, led earlier workers to regard these series of populations as belonging to several species.

The most variable character, and the one chiefly used to justify several species, is vertebral number. Arranging the data from lake populations in north-south order, there is a cline in the number of vertebrae, with no justifiable division of the populations into two or more groups (Fig. 11). There are some irregularities in the cline, but overlap of data from adjacent populations is usually substantial. The more than 250 mile geographic break between the populations in Lake Taupo and the Nelson Lakes (Rotoiti and Rotoroa) coincides with the greatest break in the cline, but this is somewhat bridged by the more southern Lake Howard population.

The vertebral cline appears to be related

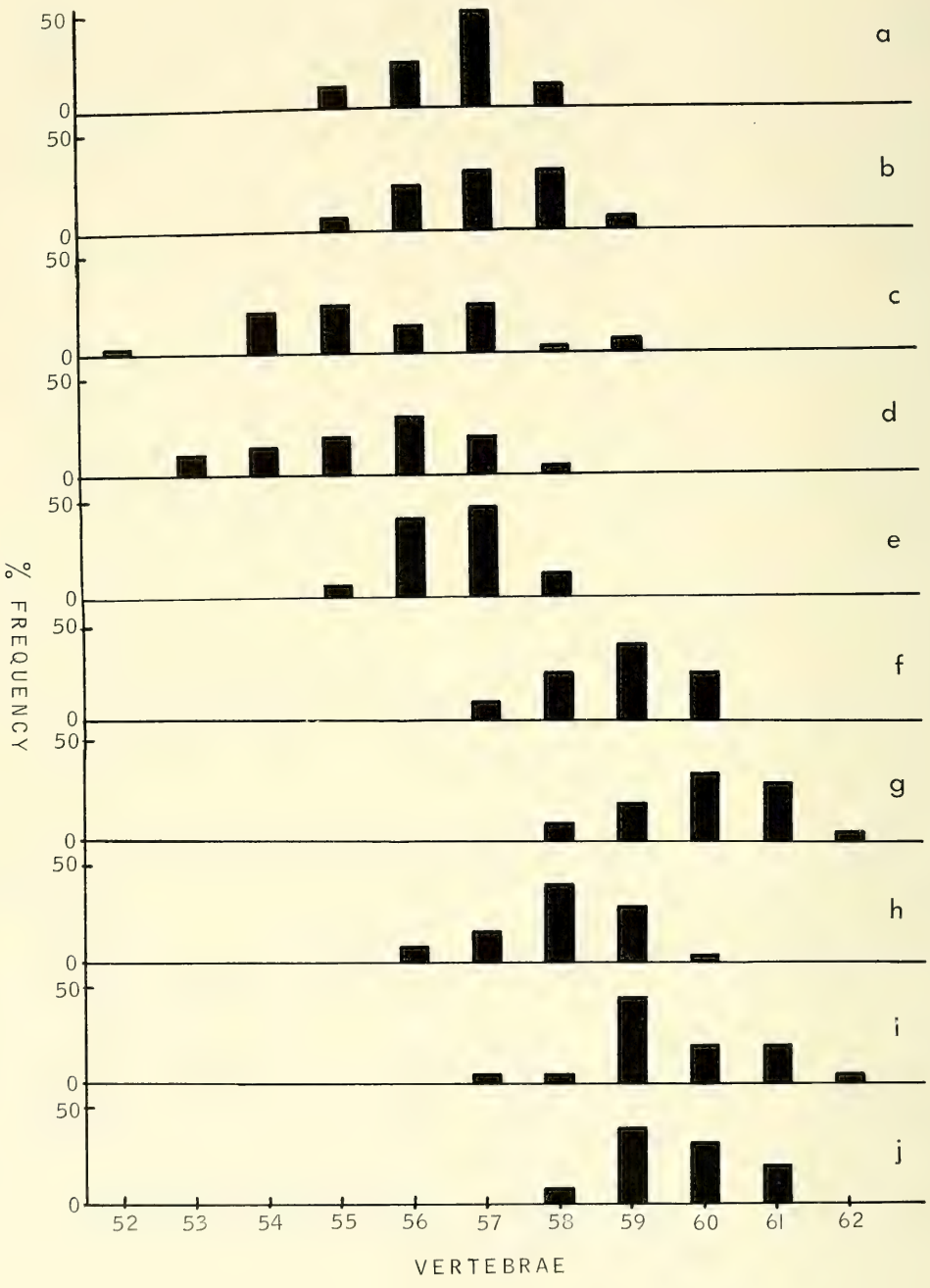

Figure 11. Variation in vertebral number in lacustrine *Galaxias brevipinnis* populations, in north-south series. a, Lake Rotorua (8 examples); b, Lake Okataina (25 examples); c, Lake Waikaremoana (27 examples); d, Lake Kiriopukae (20 examples); e, Lake Taupo (31 examples); f, Lakes Rotoroa-Rotoiti, Nelson Lakes (20 examples); g, Lake Sumner (20 examples); h, Lake Howard (25 examples); i, Lake Wanaka (20 examples); j, Lake Mahinerangi (25 examples).

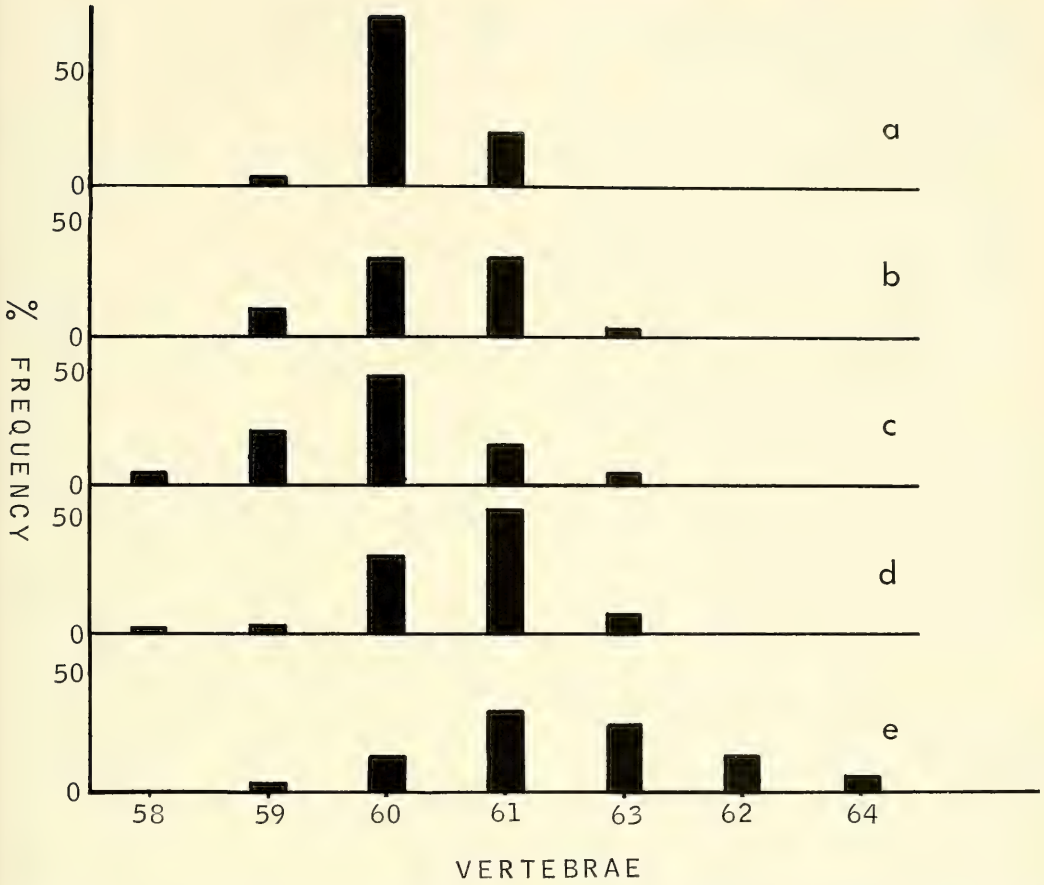

Figure 12. Variation in vertebral number in diadromous *Galaxias brevipinnis* populations. a, Northwestern North Island—North Auckland District (30 examples); b, Southern North Island—Wellington District (26 examples); c, Midwestern South Island (22 examples); d, Southwestern South Island—Haast District (36 examples); e, Sub-Antarctic Islands of New Zealand—Auckland and Campbell Islands (34 examples).

to temperatures, the number of vertebrae being lower in fishes from the more northern (warmer) lakes. Growth in these lakes is likely to be more rapid during critical developmental periods. Many workers (see Lindsey, 1961, for a recent summary) have noted the tendency for closely related species to have more parts (particularly vertebrae) towards the polar end of their range. If temperature is affecting vertebral number, then it is not a valid character for use in dividing the northern and southern population series into two species. Other meristic characters did not appear to exhibit clinal variation and varied rather irregularly, but Lindsay has noted that clinal variation in one character does not necessarily correlate with variation in another character.

Sea-going specimens were found to have about the same number of vertebrae as lacustrine examples in the more southern lakes. They exhibited variation of similar extent to that seen in other species with marine whitebait. There is slight displacement towards greater vertebral number with increasingly southern location of populations (Fig. 12, cf. *G. argenteus*, Fig.

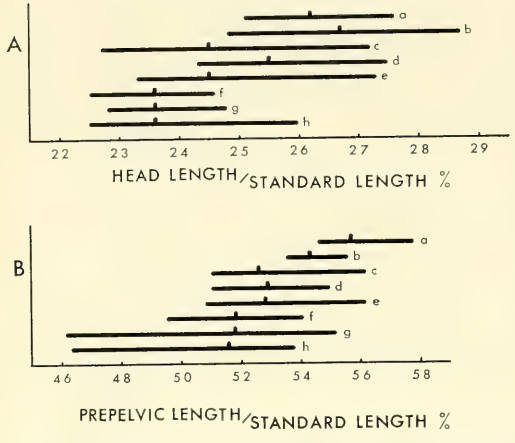

Figure 13. Variation in body proportions in lacustrine *Galaxias brevipinnis* populations. A, Head length/standard length ratio; B, Prepelvic length/standard length ratio; a, Lake Rotorua (7 examples); b, Lake Okataina (5 examples); c, Lake Waikaremoana (30 examples); d, Lake Kiriopukae (33 examples); e, Lake Taupo (18 examples); f, Lakes Rotoroa-Rotoiti, Nelson Lakes (20 examples); g, Lake Howard (21 examples); h, Lake Wanaka (20 examples).

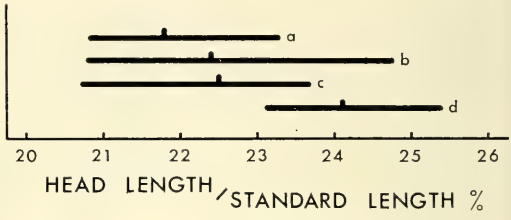

Figure 14. Variation in head length in diadromous *Galaxias brevipinnis* populations. a, Northwestern North Island—North Auckland District (9 examples); b, Southern North Island—Wellington District (23 examples); c, Western South Island (14 examples); d, Sub-Antarctic Islands of New Zealand—Auckland and Campbell Islands (21 examples).

5). The more disjunct sub-Antarctic island populations showed greater distinctness, as is predictable from their extremely southern position in the range of *G. brevipinnis*.

The most variable morphometric characters proved to be head length and prepelvic length. In lacustrine populations both head length/standard length and prepelvic length/standard length ratios exhibited north-south clinal variation, similar to that of vertebral number (Fig. 13). Variation in head length in diadromous populations showed a slight trend towards increase in length with southern displacement, again with the sub-Antarctic island populations standing somewhat apart from mainland populations (Fig. 14).

No other characters were found that distinguished any group of lake populations from any other, or the lake populations from diadromous populations. Although the inclusion of all these populations in *G. brevipinnis* results in a somewhat more variable species than some other New Zealand species of *Galaxias*, the alternative course results in two or more morphologically similar forms that differ only in clinal characters. If recognized as distinct, such species would be much more similar to each other than any other closely related species pairs in the fauna.

This is similar to the case of the Northern Hemisphere salmonids in which euryhaline diadromous populations have become locally restricted to fresh water, either voluntarily, as Atlantic salmon, *Salmo salar*, have in the Manapouri-Te Anau system in New Zealand, or by the development of downstream barriers to migration. Bigelow and Schroeder (1963: 559), for instance, recorded *Osmerus eperlanus* from both coastal-estuarine situations and landlocked situations. In some cases, as in *S. trutta* in New Zealand, the diadromous and freshwater forms mingle and may form a single gene pool. This may also occur in *G. brevipinnis*, since few of the lacustrine populations are prevented from moving downstream and interbreeding with diadromous populations. In other instances, in the northern salmonoids and in *G. brevipinnis*, populations are found to be truly landlocked and thus completely isolated geographically.

Habitat. As presently defined, *G. brevipinnis* comprises forms inhabiting a variety of types of river and lake systems. Many diadromous populations are known in lowland streams, but they may migrate a great distance inland, e.g., into tributaries of the Wanganui River on the slopes of Mount

Ruapehu at altitudes approaching 3,000 feet (900 m) and streams on Mount Egmont at more than 4,000 feet (1,200 m) (G. C. Kelly, pers. comm.). Diadromous populations occur in a few lakes, e.g., Lakes Mapourika and Kaniere, the juveniles migrating from the sea into the lakes and finally living as adults in the lake tributaries. The possibility that both lacustrine and diadromous populations occur in such lakes as these cannot at present be excluded.

Most lake populations appear to be restricted largely to the lakes and their tributaries; the juveniles shoal in the lakes and the adults inhabit the lake tributaries but are mostly absent from the lakes themselves. A fluviatile habitat is to be expected for the adults, from their obviously depressed, benthic form, adapted to rapid waters, and from the very definite upstream migration of the juveniles. Lake Howard has no tributaries, and the adults are found in the lake amongst rocks near the shore, but this seems unusual. In a few cases, e.g., Lake Coleridge, it has been found that the lacustrine populations also invade the rivers below the lakes. Lacustrine populations vary greatly in altitude, from about 200 feet (60 m) in Lake Alice to in excess of 2,000 feet (610 m) in Lakes Waikaremoana, Rotoiti (Nelson Lakes), and Monk. However, most of the lakes lie between 600 and 1,500 feet (180–460 m).

Whether diadromous or lacustrine, the adults of *G. brevipinnis* are characteristically captured from small, cold, rapidly flowing, stable, rocky streams which are often heavily overgrown with bush. The fishes are very secretive and live hidden amongst boulders in the most swiftly flowing water. In streams unmodified by clearing of the forest and agricultural development, *G. brevipinnis* may form large and dense populations.

Formation of landlocked populations. Many of the landlocked populations of *G. brevipinnis* must post-date the last Pleistocene glaciation. Fleming (1962: 89) showed that the lower limits of the ice cap in New Zealand during the last glaciation (about 15,000 years ago) would have completely engulfed many of the South Island upland lakes, in which *G. brevipinnis* is now present. Lake Mahinerangi is even more recent; Dollimore (1962: 345) reported that this lake was formed artifically as a hydro lake in 1911. Most of the lakes in the South Island occur in glacial valleys, and their formation resulted from the retreat of the ice and deposit of moraine (C. A. Fleming, pers. comm.); the now-resident fish populations must have entered the lakes since that time. If the lake populations are geographically isolated by landlocking from diadromous populations, their great morphological similarity to the diadromous form is due to the recency of their isolation. The thermal lakes are also recently formed, and their populations of *G. brevipinnis* are of very recent derivation, almost certainly post-glacial.

Life history. Little has been reported on the breeding of *G. brevipinnis.* The occurrence of a spring migration of juveniles suggests that, like other species with marine juveniles, spawning occurs predominantly in the autumn and early winter. Ripe and mature adults were most common in samples collected from March through May, although a single fully ripe female was found in a November sample. The eggs of *G. brevipinnis* are of moderate size and numerous, 1.3–1.6 mm diameter in a female 188 mm long and carrying about 7,500 eggs.

The spawning habitat has not been described, but localities from which ripe, strippable adults were collected were not different from usual adult habitats, suggesting that there may be little or no breeding migration.

On hatching, the larvae are apparently washed downstream into the sea (or lake) and develop there during the winter. The slender, transparent whitebait juveniles (Fig. 42) migrate upstream primarily dur-

Figure 15. Distribution of *Galaxias brevipinnis* (numbers in figure as in text, p. 371).

ing the spring; in diadromous populations the migration occurs concurrently with that of other whitebait species, in huge, mixed-species shoals (McDowall, 1965a: 290), although probably early in the migration period.

The transparent fishes become pigmented soon after migration. Sub-adult coloration develops initially as an overall covering of melanophores. These become concentrated along the myotomes and develop into dark, vertical chevron-shaped bands, which subsequently become subdivided to form an irregular blotching pattern. This bold blotching may persist in the adult, or may become progressively more and more fragmented to produce the vermiculations found in most adults.

Distribution. G. brevipinnis is probably the most widely distributed species of *Galaxias* in the New Zealand region. If it is shown to be conspecific with *G. weedoni*, it has trans-Tasman distribution. Coastally it is widespread, though at present, few localities are known from the east coast between East Cape and Southland. It is very common on the west coast and also in upland lakes, especially east of the main divide in the South Island, and occurs on many islands, including the very remote Chatham, Auckland, and Campbell Islands.

As with the other diadromous species, inland range is somewhat limited by physical barriers in the rivers up which the fishes migrate, but this limitation affects *G. brevipinnis* less than other galaxiids on account of its exceptional climbing ability.

Populations believed to be diadromous are known from the following localities: Mangamuka Stream (Fig. 15: 1); Merowhanara Stream, Waipoua System (2*); Waikato River (3); Te Puna Stream (4*); Whakatane River (5); Mokau River (6); Waiwakaiho River (7); Patea River (8); tributaries of the Wanganui River near Erua (9*); Ngarurоro River (10); Rangitikei River (12); Pohangina River (11, Phillipps, 1926a: 98) and Kahuterawa Stream (13), Manawatu System; Makahika River, Ohau System (14*); tributary of Otaki River at Otaki Forks (15*); Ngatiawa and Mangakotukutuku Streams, Waikanae System (16*); Horokiri Stream (17); Hutt River at Kaitoke (18); Kaiwharawhara Stream (20); Day's Bay Stream (21*); Lyall Bay and Owhiro Bay Streams (22); tributary of Lake Onoke (19); Wairau River (23); Pokororo River, Motueka System (24*); Karamea River (25); Ngakawau River (26); Buller River (27); Grey River (28); Taramakau River (29); Lake Kaniere (30); Hokitika River (31); Waitaha River (32); Wanganui River (33); Whataroa River (34); Lake Mapourika (35*); Cook River (36); Moeraki River (37); Waita River (38); Haast River (39*); Okuru and Turnbull Rivers (40); Waiatoto River (41); Arawata River (42); Jackson Bay Stream (42a*); Awarua River (43); Ethne River (44); Waitaki River (45); Clutha River (46); Chatham Islands (47, Skrzynski, 1967: 95); Campbell Island (48*); Auckland Islands (49*).

Lacustrine populations occur in the following lakes: Rotorua (50*); Rotoiti (51*); Okataina (52*); Taupo (53*); Rotopounamu (54); Rotoaira (55); Waikaremoana (56*); Kiriopukae (57*); Rotoroa (58*); Rotoiti (59*, Nelson Lakes); Bowscale Tarn (60); Sumner (61*); Taylor (62); Pearson (64, Stokell, 1949: 486); Coleridge (65*); Howard (66); Alexandrina (67); Ohau (68, Stokell, 1955: 23); Hawea (69); Wanaka (70*); Wakatipu (71); Hawdon (72, Stokell, 1949: 486); Alice and Marchant (73), and Katherine (74, all Cunningham, 1951: 74); Te Anau (75) and Manapouri (76, both Stokell, 1959a: 255); Mahinerangi (77*); Monk (78, Riney et al., 1959: 45).

The absence of lacustrine populations in the region between the southern end of the volcanic plateau and the Nelson Lakes is almost certainly attributable to the absence of upland lakes there. Otherwise, the distribution of lacustrine populations of *G. brevipinnis* is fairly continuous from the

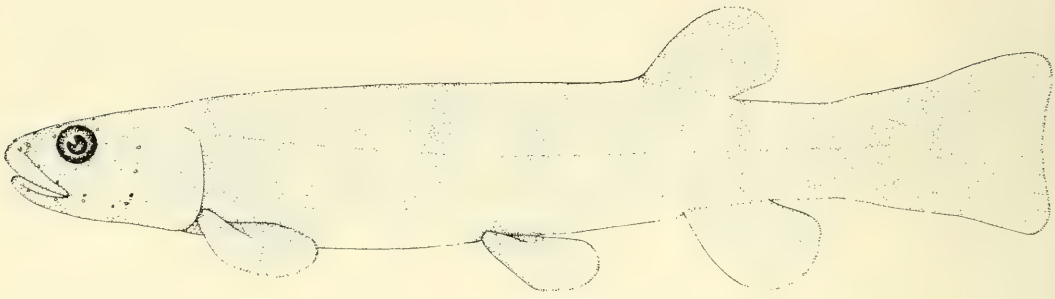

Figure 16. *Galaxias vulgaris* Stokell, 100 mm L.C.F., Maruia River, Buller River System.

most northern lakes of the volcanic plateau to southernmost Fiordland.

Galaxias vulgaris Stokell, 1949
Figure 16

Galaxias vulgaris Stokell, 1949: 491 (holotype: CMCNZ 72, seen; paratype: DMNZ 2069, not seen; locality: Rubicon River, Springfield, Canterbury).

Galaxias anomalus Stokell, 1959b: 265 (holotype: DMNZ 2776, seen; locality: the outlet of a spring which is drained by a ditch crossing the Ophir-Omakau Road a few chains north-east of the Ophir Hotel[1]).

Diagnosis. Differs from *G. brevipinnis* Günther (Fig. 10) in characters noted in the diagnosis of that species (p. 363).

Taxonomy. Stokell (1949: 491, 1959b: 256) has recognized two moderately large and slender species from upland, eastern South Island streams, in addition to *G. brevipinnis.* Populations of fishes of this type are present in most of the major river basins in the east of the South Island, from the Conway River south to the Waiau (Southland), and collection localities are numerous. *G. vulgaris* was recorded by Stokell from Canterbury, the Waiau River (Kaikoura) to the Rakaia, and *G. anomalus* from streams in Central Otago. He did not discuss differences between *G. anomalus* and *G. vulgaris,* but the chief differences between his descriptions of the two species are head length—4.2–4.8 in standard length in *G. vulgaris* and 5.1–5.3 in *G. anomalus*—and in the length of the gill rakers—"long" and "very short" respectively. The two species are indistinguishable from meristic data published by Stokell. Examination of samples from 15 localities indicated that they form a single rather variable species such that the differences between *G. vulgaris* and *G. anomalus,* as defined by Stokell, are absorbed in inter-populational differences. The holotype of *G. anomalus,* though recorded from a drain, is typical of *G. vulgaris* as found in the shingly streams of the upper Clutha River system.

Description. Trunk moderately slender, belly often deepened and rounded, somewhat flattened dorsally with moderate development of a middorsal furrow, trunk profiles somewhat parallel; depressed anteriorly on head, somewhat more slender posteriorly on caudal peduncle, which is moderately long, and somewhat longer than deep. Lateral line a moderately developed midlateral groove, accessory lateral line not observed. Head long and blunt, rounded, much broader than deep. Lower jaw receding a little; jaws long in head, cleft moderately oblique, reaching to about middle of eye; lower jaw profile from ventral aspect moderately broad and shallow. Eye of moderate size, towards upper head profile, interorbital convex to flat.

[1] Omakau is almost directly north of Ophir; the Ophir-Omakau Road at the Ophir Hotel runs in a northwest–southeast direction, so that I could find no locality agreeing with Stokell's description. This area is a part of the Mahinurikia catchment, a Clutha River tributary, and samples were collected in this catchment, not far from Ophir.

Jaws with moderate development of canines laterally; mesopterygoidal teeth strong; pyloric caeca long; gill rakers weak to moderate.

Fins small and fleshy; median fins short-based, but fin extending well toward caudal base, well-rounded distally; anal origin well behind dorsal origin. Pelvic fin inserted somewhat behind midpoint of standard length, fin moderately long in pelvic-anal interval, which is long. Pectoral fin inserted low lateroventrally, fin lamina usually directed ventrally; fin of moderate length and rounded in outline with middle rays longest. Caudal fin moderately long, emarginate, lobes of fin rounded, depth about equal to body depth; caudal peduncle flanges moderately developed.

Coloration. Basic body color brownish to olive, trunk covered dorsally and laterally with irregular and variably dense vermiculations, these disappearing ventrally, sometimes bold blotches, regular chevron-shaped bands, or grading to an almost uniform darkening on the dorsal and dorsolateral trunk.

Size. G. vulgaris has been found up to 150 mm long, and seems to commonly reach 100–115 mm.

Variation. Meristic: dorsal 7 (4), 8 (74), 9 (106), 10 (24), 11 (1); caudal 14 (15), 15 (12), 16 (163), 17 (4), 18 (2); anal 8 (7), 9 (54), 10 (96), 11 (29), 12 (4); pelvic 6 (4), 7 (174), 8 (13); pectoral 10 (2), 11 (27), 12 (68), 13 (70), 14 (18), 15 (7), 16 (2); branchiostegals 5 (1), 6 (12), 7 (130), 8 (39), 9 (2); vertebrae 49 (3), 50 (28), 51 (75), 52 (144), 53 (99), 54 (60), 55 (18), 56 (1), 57 (1); gill rakers 2–7 (2), 2–8 (5), 2–9 (3), 2–10 (4), 3–6 (1), 3–7 (9), 3–8 (36), 3–9 (36), 3–10 (10), 4–7 (1), 4–8 (7), 4–9 (8). Morphometric: see Table 2, p. 365.

Population differences. As I define the species, *G. vulgaris* is rather variable, comparable in variability to *G. divergens* and *N. apoda.* These three species are also the most wide-ranging species that are confined to fresh water and which are thus less able to disperse from one river basin to another, by marine routes. Gene flow tends therefore to be limited to population exchanges by means of stream capture and perhaps occasional extraordinary flood situations, when waters of two neighboring catchments become confluent temporarily. In recent years, contact between river systems has been increased by the construction of irrigation canals that transfer water from one catchment to another, but nothing is known of the effect of these changes on the populations of *G. vulgaris.*

The magnitude of variability in *G. vulgaris* can be seen in Figures 17–19, in which various morphological characters are shown with the populations listed in approximately north–south order. It is not easy to arrange the populations in an order likely to express a temperature gradient, since the nature of the watersheds in which these populations occur and their altitude in the headwaters are very variable, even in cases of closely adjacent localities; e.g., the Hinds River drains coastal hills, whereas the nearby Ashburton River penetrates deep into the Southern Alps, which reach well over 7,000 feet in the headwaters of the river. Similarly in the Clutha River System, the Poolburn and Cardrona Rivers are at similar altitudes, but the Poolburn derives its water from the low Rough Ridge, rising to less than 3,500 feet, whereas the Cardrona drains the higher Crown Range, reaching more than 6,000 feet. In comparing populations from the various rivers and trying to relate differences to water temperatures, it is important to realize that even though populations may have occurred at similar altitudes, or be in close proximity to each other, temperatures may be very different, because of the origin of the water. Water temperatures will be a function of altitude, latitude, and the nature of the watershed in the hinterland of the river, and since there is no way to relate these factors and predict water temperatures, it is not pos-

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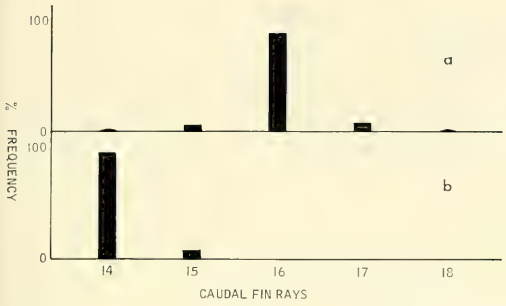


Figure 18. Variation in caudal fin ray number in *Galaxias vulgaris*. a, Other populations of *Galaxias vulgaris* (190 examples); b, Linnburn Stream, Taieri River System (15 examples).

sible to relate character differences to water temperatures. Vertebral number, which responds to temperature differences, was found to be very variable, but this variation was irregular; most populations were found to have a range of three to five vertebrae (Fig. 17).

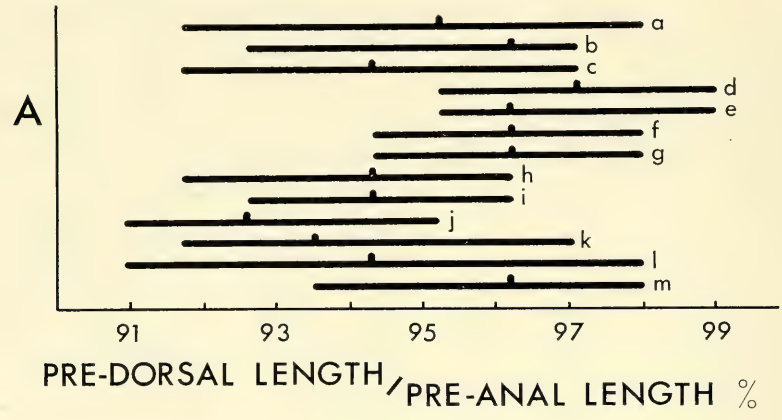
The most distinctive population in the series examined was from the Linnburn Stream, above the Waipori Falls in the Taieri River System. It is distinctive chiefly in the number of caudal fin rays, usually a stable character with 16 rays, but reduced to 14, or occasionally 15 in the Linnburn fishes (Fig. 18). In other meristic characters, this population is "normal." Body depth at vent/standard length and depth of caudal peduncle/length of peduncle ratios for the Linnburn fishes showed that they are stouter than other populations in this species (Fig. 19B). Head length/standard length ratio is also higher than in most, but several other populations, e.g., those in the Hurunui and Cardrona Rivers (Fig. 19C) were also found to differ considerably from the bulk of the populations studied.

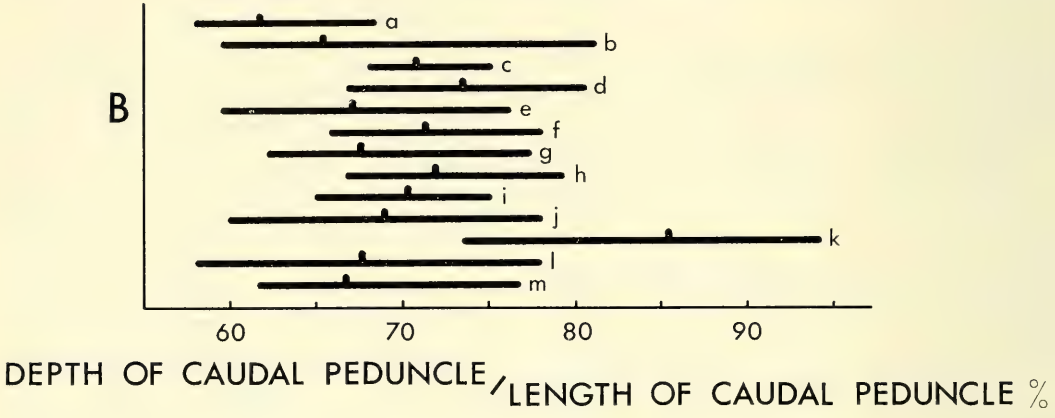
In some of the more variable morphometric characters, somewhat clinal change is exhibited along a north-south axis, although various and different populations were found to be aberrant and not to relate to the general trends. Head length/standard length (Fig. 19C), length of caudal peduncle/standard length and pre-dorsal/pre-anal length (Fig. 19A) ratios were all found to exhibit this tendency to some extent. These differences cannot justifiably be related to temperature or any other ecological parameter, with our present understanding of the species.

Coloration was found to vary greatly. As in other characters, the Linnburn population was most unusual, being much darker, the trunk patterning almost black. In this species, color pattern seems to be related to habitat. The more northern Canterbury populations occurred in swift, shingly streams in wide, open valleys, with sometimes milky water derived from snow fields. These fishes tended to have olivaceous coloration and a diffuse color pattern. Further to the south, the fishes from Central Otago were much more boldly colored, the vermiculations being similar in form to those in the Canterbury fishes, but contrasting much more with the ground color. These fishes were generally collected from small, stable, clear-flowing streams, and these color differences appear to be related to differences in lighting conditions in the respective habitat types—diffuse, dim but rather constant lighting in the open but somewhat murky alpine Canterbury streams, but broken lighting, interrupted also by marginal stream cover, in the clear flowing Central Otago streams.

←

Figure 17. Variation in vertebral number in *Galaxias vulgaris*, localities in north-south order. a, Conway River (31 examples); b, Waiau River (27 examples); c, Maruia River, Buller River System (26 examples); d, Hurunui River (18 examples); e, Rakaia River (19 examples); f, Ashburton River (29 examples); g, Hinds River (25 examples); h, Waitaki River (28 examples); i, Cardrona River, Clutha River System (35 examples); j, Shag River (33 examples); k, Poolburn River, Clutha River System (41 examples); l, Totara Stream, Taieri River System (15 examples); m, Linnburn Stream, Taieri River System (15 examples); n, Aparima River (28 examples); o, Wilanda Downs Stream, Waiau River System (Southland) (40 examples).





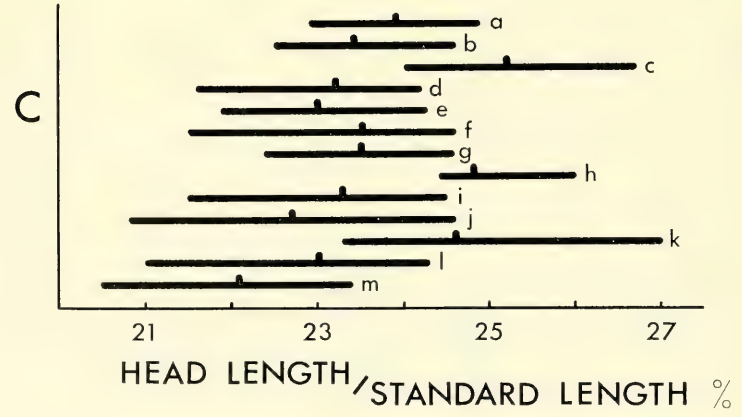


Figure 19. Variation in body proportions in *Galaxias vulgaris*, localities in north-south order. A, Predorsal length/preanal length ratio; B, Depth of caudal peduncle/length of caudal peduncle ratio; C, Head length/standard length ratio; a, Conway River (15 examples); b, Waiau River (15 examples); c, Maruia River, Buller River System (15 examples); d, Hurunui River (15 examples); e, Rakaia River (13 examples); f, Ashburton River (30 examples); g, Hinds River (15 examples); h, Cardrona River, Clutha River System (15 examples); i, Shag River (15 examples); j, Poolburn River, Clutha River System (15 examples); k, Linnburn Stream, Taieri River System (14 examples); l, Aparima River (15 examples); m, Wilanda Downs Stream, Waiau River System (Southland) (15 examples).

This is an interesting species, in which the study of inter-populational variation appears to be potentially profitable and to warrant further investigation. Since the populations occur in widely separated river basins, it is probable that at least some of the variation is simply a product of mosaic evolution. Further examination of the Linnburn population may, however, show that subspecific or specific distinctness has been attained.

Habitat. *G. vulgaris* lives normally in water type similar to that in which *G. brevipinnis*, *G. prognathus*, and particularly *G. paucispondylus* are found. In Canterbury, most of the cold upland rivers thread their way back and forth over broad, unstable flood plains. *G. vulgaris* occurs commonly in these rivers and their tributaries, mostly in the very fast and broken water. Further south, in Central Otago and Southland, the terrain is more stable, and the upland rivers are usually narrower and more strictly confined to their river courses. In these rivers and their tributaries, *G. vulgaris* also occurs in the rapid and broken water. It has generally not been found in streams entering lakes, although the Hurunui River, above Lake Sumner, is an exception.

G. vulgaris is a typical, highly secretive galaxiid, and is found in the interstices of boulder rapids; it sometimes hides in marginal cover, where this is present. The claim has been made that *G. anomalus* can withstand droughts, like the mudfishes (*Neochanna* species), but I know of nothing to substantiate it, and I think it is doubtful that a species usually found in cold, swiftly flowing streams can aestivate.

Life history. *G. vulgaris* is restricted throughout its life to flowing fresh waters, it has no whitebait juvenile, and probably has no migration of any magnitude. Larvae have often been collected with the adults, suggesting that spawning occurs in or near the customary adult habitat.

Samples collected in December and January invariably contained only spent or rejuvenating fishes; some collected in April and May were showing considerable advance towards gonad maturity, while samples collected in October were mostly freshly spent, although a few individuals were ripe. Recently hatched larvae, 10–15 mm long, were collected in December. These data all suggest that spawning occurs in the early and middle spring, agreeing partly with Stokell's (1955: 25) observation of spawning in winter and early spring. The larvae may be found swimming in small groups in backwaters and slack water at the edges of the streams.

The eggs are moderately large, measuring about 1.5 mm diameter when ripe, and relatively few in number. The largest ripe female examined was 83 mm long and contained 865 eggs.

Distribution. *G. vulgaris* occurs only in the South Island, chiefly on the east of the Southern Alps and the Kaikoura Ranges, but it has extended its range over the alps into the upper Buller River System. It is known from the following localities: Upper Buller River System near Maruia Springs (Fig. 20: 1*); Conway River (2*); Mason, Wandle, and Leeds Rivers, Waiau River System (3*); Hurunui River above Lake Sumner (4*); Cass River (5), Porter River (7), and Rubicon River (8) in the Waimakariri River System (Stokell, 1949: 491); Ashley River and Selwyn River (Stokell, 1949: 491); Wilberforce River (6) and Harper and Avoca Rivers (6a*), Rakaia River System; North Branch (9*) and Taylor's Stream (10*), Ashburton River System; Hinds River (12*); Rangitata River at Mesopotamia (11*); Orari River at Peel Forest (13); Haehaemoana River, Opihi River System (14); tributary of Lake Pukaki (Stokell, 1955: 25); Waitaki River at Otematata (15*); Shag River (17*); Swinburn (18*), Totara (20*), and Linnburn (21*) Streams, Taieri River System; Cardrona (16*) and Poolburn (19*) Streams, Clutha River System; Mataura River (22); Aparima River (23*); Orawia

Figure 20. Distribution of *Galaxias vulgaris* (numbers in figure as in text, p. 377).

River and Waiau River at Wilanda Downs (24*).

Galaxias maculatus (Jenyns, 1842)
Figure 21

Mesites maculatus Jenyns, 1842: 119 (holotype: BMNH 1917.7.14.6, not seen; paratypes (3): BMNH 1917.7.14.7–9, not seen; locality: fresh water brook, Hardy Peninsula, Tierra del Fuego).

Mesites attenuatus Jenyns, 1842: 121 (holotype: BMNH 1917.7.14.11, not seen; locality: fresh water, Bay of Islands, New Zealand); Richardson, 1843: 26.

Galaxias attenuatus: Valenciennes, *In* Cuvier and

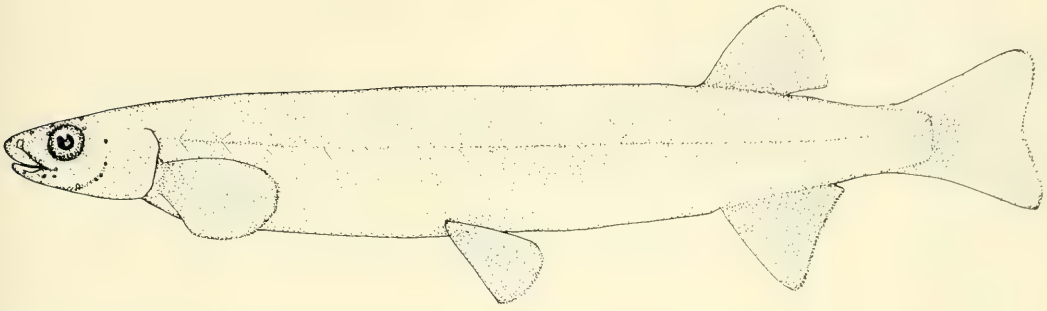


Figure 21. *Galaxias maculatus* (Jenyns), 94 mm L.C.F., Ship Creek, South Westland.

Valenciennes, 1846: 348; Günther, 1866: 210; Hutton, 1872: 60, 1896: 317; Clarke, 1899: 78; Hutton, 1904: 51; McKenzie, D. H., 1904: 122; Regan, 1905: 368; Phillipps, 1919: 211, 1924a: 117, 1926b: 292, 1927a: 13; Hope, 1928: 389; Stokell, 1949: 479; McDowall, 1967b, 1968b.

Galaxias forsteri: Kner, 1865: 320 (not *G. forsteri* Valenciennes, *In* Cuvier and Valenciennes, 1846: 351).

Austrocobitis attenuatus: Ogilby, 1899: 158.

Galaxias maculatus attenuatus: Stokell, 1966: 78.

Diagnosis. Differs from *G. usitatus* McDowall (Fig. 23) in having more vertebrae and pelvic fin rays, shorter head with smaller eye, longer pelvic-anal interval, and the presence of a marine whitebait stage. Differs from *G. gracilis* McDowall (Fig. 24) in having a much higher vertebral count, more dorsal fin rays, more branchiostegals and many fewer gill rakers; also in more anterior pelvic fin insertion, shorter pelvic-anal interval, much shorter head, broader interorbital, and smaller eye.

Description. Slender bodied, trunk rounded, somewhat compressed and deeper than broad, much more slender on head and on caudal peduncle, which is short and very slender, depth much less than length. Lateral line a well-developed mid-lateral furrow; accessory lateral line not evident. Head small and slender, short; eye large, moderately deep in head, interorbital convex and moderately broad in head width, but head itself narrow; jaws short, about equal in length, cleft reaching to about anterior eye margin, slightly oblique, gape very narrow; profile of lower jaw from ventral aspect deep and rather narrow, U-shaped. Canine teeth lacking from jaws; mesopterygoidal teeth well developed; gill rakers well developed; pyloric caeca rudimentary or absent.

Median fins rather small, membranous. Dorsal fin origin well back, fin short based, greatest length not much greater than basal length, distal margin of fin somewhat rounded. Anal origin more or less below dorsal origin, greatest fin length very little greater than basal length, distal margin of fin straight or concave, inclined to trunk axis, anterior rays much the longest. Pectoral fin short in rather long pectoral-pelvic interval, fin inserted high laterally. Pelvic fins very short in long pelvic-anal interval, insertion somewhat behind midpoint of standard length. Caudal fin short, forked, depth sub-equal to body depth; caudal peduncle flanges weakly developed.

Variation. Meristic: dorsal 9 (7), 10 (58), 11 (59), 12 (4), 13 (2); caudal 15 (1), 16 (80); anal 14 (7), 15 (31), 16 (53), 17 (36), 18 (5); pelvic 6 (1), 7 (80); pectoral 11 (4), 12 (28), 13 (62), 14 (17), 15 (3); branchiostegals 5 (9), 6 (93), 7 (73), 8 (5); vertebrae 59 (1), 60 (13), 61 (44), 62 (45), 63 (24), 64 (5); gill rakers 3–10 (2), 3–11 (3), 4–10 (10), 4–11 (15), 4–12 (3), 5–10 (4), 5–11 (1), 5–12 (1). Morphometric: see Table 3, p. 380.

Coloration. Trunk pale creamish white, covered with greenish gray mottling dorsally and laterally, mottling failing laterovventrally and ventrally and varying from

Table 3. Morphometric variation in shoaling species (figures given as percentages of denominator of ratio).

	G. maculatus			*G. usitatus*			*G. gracilis*		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	87.7	90.9	91.7	88.5	89.3	90.1	87.7	89.3	91.7
B.D.V./S.L.	10.3	11.6	12.9	9.9	11.5	13.0	10.5	11.2	12.1
L.C.P./S.L.	8.8	10.5	12.3	8.6	9.9	10.9	10.4	11.8	13.4
D.C.P./L.C.P.	49.0	59.5	68.5	59.2	66.7	76.3	48.1	54.4	64.9
Pre D./S.L.	74.6	76.9	78.7	74.1	76.3	78.7	73.0	74.6	78.1
Pre D./Pre A.	96.2	99.0	102.0	96.2	98.0	101.0	97.1	100.0	103.1
D.F.B./S.L.	7.8	9.1	11.3	8.5	10.1	12.5	7.2	7.9	9.2
D.F.B./D.F.M.	58.5	70.4	82.0	61.0	68.5	77.5	58.5	65.8	72.5
A.F.B./S.L.	11.8	13.7	15.6	12.2	13.6	15.1	13.0	14.2	15.5
A.F.B./A.F.M.	78.1	84.0	90.9	75.2	81.3	87.0	75.2	84.8	90.1
Pre Pel./S.L.	48.8	50.9	52.9	49.5	52.9	55.6	53.1	54.6	56.2
Pec.Pel./S.L.	29.9	32.2	34.7	27.5	30.3	33.1	28.4	31.4	35.1
Pec./Pec.Pel.	30.7	35.3	42.2	35.6	39.0	43.2	32.3	36.9	42.4
Pel.An./S.L.	24.4	27.7	30.2	21.9	25.4	27.2	20.0	21.6	24.0
Pel./Pel.An.	29.4	36.8	44.0	37.1	43.4	49.1	40.9	45.6	50.0
H.L./S.L.	18.5	20.0	21.6	22.0	23.5	24.6	22.8	24.3	25.5
H.D./H.L.	43.7	48.8	52.9	42.9	46.3	50.0	42.9	48.1	52.4
H.W./H.L.	45.1	51.6	56.2	43.7	48.8	53.5	46.7	49.3	53.5
Sn.L./H.L.	26.5	28.5	33.3	25.9	28.7	32.6	25.9	27.9	31.3
P.O.H.L./H.L.	48.5	53.2	58.5	49.0	50.3	53.8	50.0	54.4	59.2
Io.W./H.L.	34.3	37.6	41.3	30.8	33.9	37.5	28.6	31.0	33.2
D.E./H.L.	19.5	21.8	23.7	21.8	24.3	26.9	22.2	24.3	27.3
L.U.J./H.L.	28.4	31.1	35.7	31.7	34.4	37.0	28.0	30.8	34.1
L.M./H.L.	25.6	28.7	32.5	28.6	32.9	36.9	26.1	28.5	33.3
W.G./H.L.	25.0	29.0	32.9	26.3	28.9	34.5	25.0	27.1	30.4
Fish examined		40			20			30	

fine speckling to bold, irregular blotches. The belly, opercular covers, and eyes are silvery. The head is usually darker than the rest of the trunk, the fins almost colorless, except for a few melanophores along the fin rays and at the base of the caudal fin.

Size. *G. maculatus* is known to grow to 169 mm, and commonly reaches 100–110 mm.

Population differences. Examination of 80 fishes from the Waikanae River and 51 from the Awarua River, localities about 400 miles apart, revealed no meristic differences between these populations. Samples from more distant Australian and South American populations have shown that there are clinal differences in some characters (McDowall, 1967b).

Habitat. *G. maculatus* is found in diverse habitat types, but appears to be most successful in small, stable, coastal and lowland streams, chiefly in gently flowing water, usually above tidal influence. Large shoals are often found in back-waters and similar areas where the water is slack. It is abundant in the darkly tannin-stained waters of bush and flax swamps and streams on the west coast of the South Island. However, *G. maculatus* inhabits a wide variety of water types, including quite swift, gravelly streams, where the shoals appear to break up, and the fish are usually found singly, or in twos and threes in cover at the stream margins. Upstream range of *G. maculatus* is usually very limited. Compared with other galaxiids, it has very poor climbing ability, and it is limited to streams below falls that other whitebait species are able to surmount. *G. maculatus* is probably the most prolific, open-living, and commonly encountered species of *Galaxias*.

Figure 22. Distribution of *Galaxias maculatus*.

Life history. Because of its economic importance in the New Zealand whitebait fishery, the life history of *G. maculatus* has been extensively studied (Hayes, in Hefford, 1931a, b, 1932; McKenzie, M. K., n. d.; Benzie, 1961; Burnet, 1965; McDowall, 1968b).

G. maculatus is peculiar in that it breeds amongst grasses on estuarine flats and that breeding occurs in synchrony with the high spring tides. The ripe fish migrate downstream into estuaries in large shoals and swim out over tidal flats covered by the exceptional tides at the full and new moons. The eggs are deposited amongst the bases of terrestrial plants, mostly grasses and sedges, and are left exposed when the tide recedes. They hatch at subsequent spring tide cycles and the larvae are washed out into the sea. The

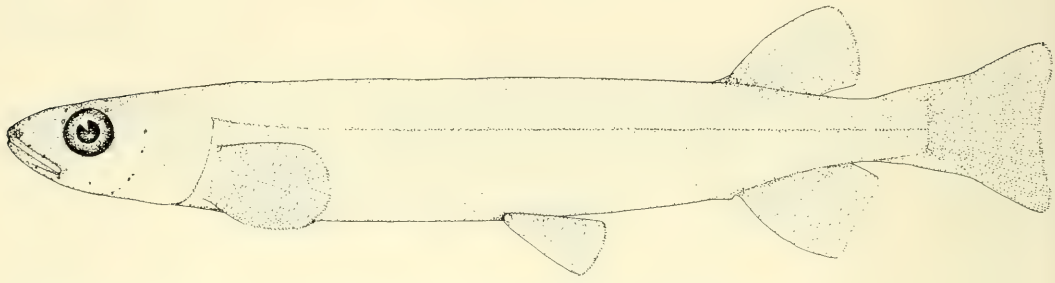


Figure 23. *Galaxias usitatus* McDowall, 72 mm L.C.F., Lake Waiparera, North Auckland.

eggs will tolerate and hatch in water of salinities varying between pure fresh and pure sea water. Spawning is reported from September to June, but occurs mostly in the autumn, from March to May. The transparent whitebait juveniles (Fig. 40) migrate into fresh water during all months of the year, but most commonly in the spring, from August to November. Size at migration is mostly between 45 and 55 mm. The marine life lasts over the winter period between the autumn spawning and the subsequent spring migration. Most adults reach maturity at one year and are thought usually to breed only once. In exceptional cases, maturation is delayed for a further one or even two years, and some fish may survive an initial spawning and perhaps spawn again.

The eggs are small, measuring about 1 mm diameter when ripe, but size is variable. Fecundity was found to vary from 137 to 13,000 in fishes between 47 and 135 mm long (McDowall, 1968b). Compared with other galaxiids examined, egg number is high.

Distribution. *G. maculatus* is known from all over New Zealand, in coastal situations, and also on the Chatham Islands. It occurs in southeastern Australia, Tasmania, Lord Howe Island, Southern Chile, Patagonia, and the Falkland Islands. With *Geotria australis*, the southern lamprey, which has a similar range, it is probably the most widely dispersed species of freshwater fish known (Fig. 22).

Galaxias usitatus McDowall, 1967
Figure 23

Galaxias usitatus McDowall, 1967a: 7 (holotype: NZMD, seen; paratypes: DMNZ 4,500, seen; MCZ 45054, seen; USNM 201223, seen; locality: Lake Waiparera, near Kaitaia, North Auckland).

Diagnosis. Differs from *G. maculatus* (Jenyns) (Fig. 21) in characters noted in the diagnosis of that species (p. 379); differs from *G. gracilis* McDowall (Fig. 24) in having more vertebrae, more branchiostegals, fewer gill rakers, a shorter pelvic-anal interval, longer dorsal fin base, shorter caudal peduncle, the presence of serrations on the free margin of the operculum and the greater size attained.

Description. Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle, which is slender and short. Lateral line an indistinct midlateral furrow; accessory lateral line not evident. Head long and slender, about as broad as deep. Eye large, close to upper head profile, interorbital more or less flat, broad relative to head width. Jaws equal and prominent, cleft slightly oblique, reaching to about anterior eye margin, gape rather narrow; profile of lower jaw from ventral aspect a deep and rather narrow U. Jaws without canines; mesopterygoidal teeth well developed; pyloric caeca lacking; gill rakers well developed; free margin of opercular membrane finely serrate.

Fins membranous and short, except anal, which is long based. Dorsal fin origin well

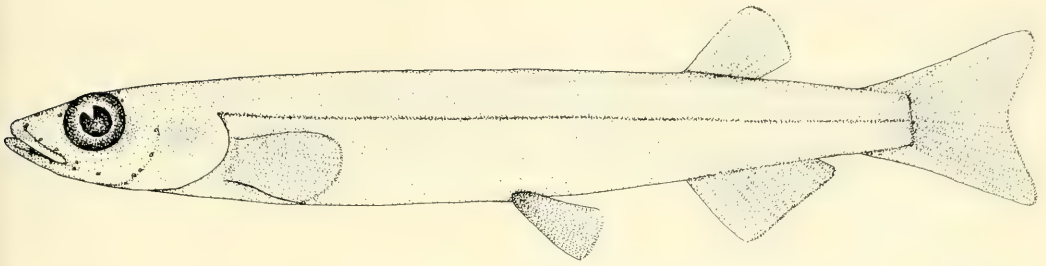


Figure 24. *Galaxias gracilis* McDowall, 59 mm L.C.F., Upper Lake Rototuna, North Auckland.

back, fin with moderately short base, maximum fin length somewhat longer than fin base, distal margin of fin slightly rounded. Anal fin origin more or less below dorsal origin; fin long based, but greatest fin length little greater than basal length, distal margin of fin about straight, inclined to trunk axis. Pelvic fin inserted at about midpoint of standard length, pelvic-anal interval short, pelvic fin moderate in pelvic-anal interval, short. Pectoral fin short, inserted rather high laterally. Caudal fin very short, forked, fin depth about equal to body depth; peduncle flanges poorly developed.

Variation. Meristic: dorsal 9 (2), 10 (22), 11 (15), 12 (2); caudal 14 (1), 15 (4), 16 (34), 17 (1), 18 (1); anal 12 (3), 13 (8), 14 (6), 15 (3), 16 (1); pelvic 6 (30), 7 (11); pectoral 11 (1), 12 (5), 13 (21), 14 (12), 15 (2); branchiostegals 5 (1), 6 (25), 7 (15); vertebrae 54 (2), 55 (5), 56 (10), 57 (12), 58 (9), 59 (3); gill rakers 4–11 (2), 4–12 (6), 4–13 (1), 5–11 (5), 5–12 (6). Morphometric: see Table 3, p. 380.

Coloration. Trunk a dusky gray-brown and covered with irregular dark blotches, very similar to *G. maculatus.* In fresh specimens, the lateroventral and ventral abdomen are silvery, but in preserved material, colorless.

Size. G. usitatus is known to grow to 81.5 mm. Examples from a sample collected from the type locality were commonly 60–70 mm long.

Population differences. Only one population of *G. usitatus* is presently known.

Habitat. G. usitatus was collected along the shores of Lake Waiparera, mostly amongst moderately open sedges growing in a few inches to a foot of water. It was also collected in a small, boggy, overgrown tributary that drains partly cleared manuka (*Leptospermum* sp.) scrublands. It is mostly a midwater swimming and shoaling species.

Life history. Nothing is known of the breeding of *G. usitatus,* except that it must occur either in the lake or in the small tributary stream running into the lake. Population size in the tributary stream in March, when specimens were collected, was extremely low, so that if spawning does occur there, a definite spawning migration of some type must take place. Examination of the gonads showed that in March, the fish are approaching maturity, although breeding appeared to be some time away. The gonads were too immature for useful measurements of eggs or determination of egg number. The eggs appeared to be quite numerous, comparable in number with those of *G. maculatus* of similar size. From the stage of maturity, breeding appears likely to occur in late autumn or early winter.

Distribution. G. usitatus is presently known only from Lake Waiparera, the type locality, and a small stream entering the lake from the south (Fig. 25).

Galaxias gracilis McDowall, 1967
Figure 24

Galaxias gracilis McDowall, 1967a: 6 (holotype: NZMD, seen; paratypes: DMNZ 4499, seen; MCZ 45053, seen; USNM 201224, seen; locality: Upper Lake Rototuna, Kaipara Harbour, North Auckland).

Diagnosis. Differs from *G. maculatus* (Jenyns) (Fig. 21) and *G. usitatus* McDowall (Fig. 23) in characters discussed in the diagnoses of these species (pp. 379 and 382 respectively).

Description. Trunk cylindrical, slender, somewhat depressed on head, laterally compressed on caudal peduncle, somewhat deeper than broad. Caudal peduncle short and slender. Lateral line an indistinct lateral furrow; accessory lateral line not evident. Eye large; at upper head profile, interorbital flat, very narrow. Lower jaw protruding a little or equal in length to upper; lips thin, cleft of mouth slightly oblique, extending to about anterior eye margin; gape very narrow, lower jaw from ventral aspect deep and narrow, U-shaped. Jaws without canines; mesopterygoidal teeth moderately developed; gill rakers long; pyloric caeca lacking.

Fins membranous and short, except anal, which is rather long based; anal origin more or less below dorsal origin. Distal margin of dorsal fin rounded to straight, anterior rays longest; margin of anal straight, anterior rays longest, maximum fin length little greater than basal length. Pelvic fins inserted rather posteriorly, pelvic-anal interval short, fin relatively short in pelvic-anal interval. Pectoral fin short, inserted high laterally. Caudal fin short, forked, depth about equal to body depth; caudal peduncle flanges poorly developed.

Variation. Meristic: dorsal 7 (2), 8 (23), 9 (22), 10 (3); caudal 15 (4), 16 (42), 17 (4); anal 12 (2), 13 (7), 14 (29), 15 (13), 16 (1); pelvic 6 (7), 7 (40), 8 (3); pectoral 12 (8), 13 (28), 14 (14); branchiostegals 4 (2), 5 (27), 6 (21), 7 (2); vertebrae 47 (1), 48 (16), 49 (24), 50 (9); gill rakers 5–13 (2), 5–14 (2), 5–15 (1), 6–13 (1), 6–14 (12), 6–15 (7), 6–16 (3), 6–17 (1), 7–16 (1). Morphometric: see Table 3, p. 380.

Coloration. Trunk densely covered with large melanophores that intensify on the head and dorsum of the trunk, failing lateroventrally and ventrally. Fresh specimens are silvery in these latter areas.

Size. G. gracilis is known to grow only to 62.5 mm. Many examples in the very large sample collected were between 45 and 55 mm long, but few were larger.

Population differences. Only one population of *G. gracilis* is known.

Habitat. G. gracilis has been collected only from a small, coastal dune lake. Large numbers were collected from shallow water near the lake shore.

Life history. The entire life history of *G. gracilis* occurs in fresh water, since the locality from where it is known is landlocked. Ripe males were present in the sample, collected in March, but no ripe or mature females. Breeding thus appears likely to occur some time in the autumn. In a female 47 mm long and approaching maturity, there were 604 eggs, 0.6–0.8 mm in diameter.

Distribution. G. gracilis is presently known only from the type locality, Upper Lake Rototuna (Fig. 25).

Galaxias divergens Stokell, 1959
Figure 26

Galaxias divergens Stokell, 1959b: 266 (holotype: DMNZ 2777, seen; locality: a rapid shingly stream flowing into the Maruia River about a mile west of the hot springs).

Diagnosis. Very similar in form to *G. paucispondylus* Stokell (Fig. 29) but differs in its stouter build, slightly shorter caudal peduncle, and more posterior pelvic fin insertion. The chief differences are the very reduced gill rakers and the lower number of fin rays in the pelvic and caudal fins. Differs from *G. prognathus* Stokell (Fig. 31) in its stouter build, the jaws being sub-equal with the upper jaw longer

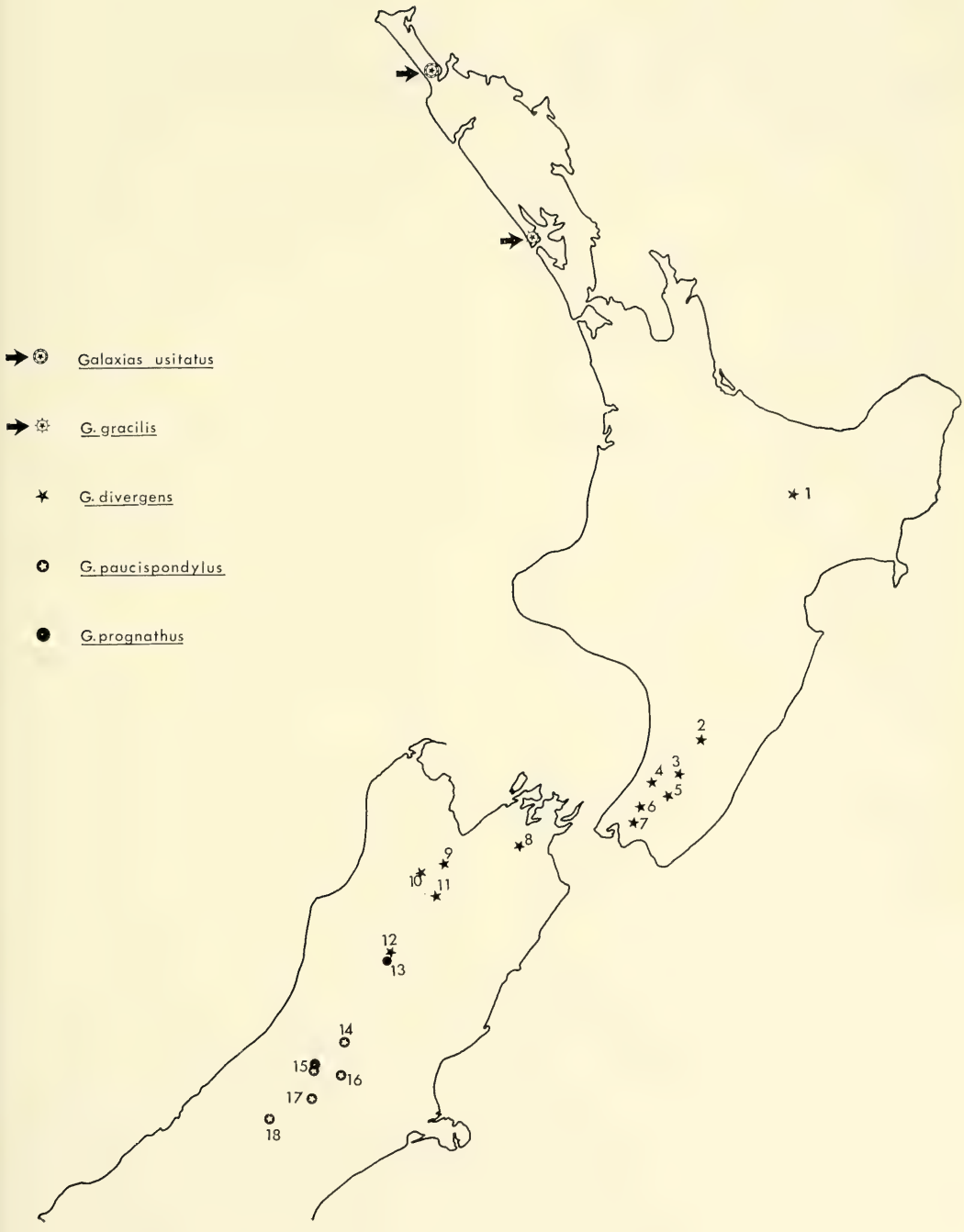


Figure 25. Distribution of *Galaxias usitatus*, *G. gracilis*, *G. divergens*, *G. paucispondylus*, and *G. prognathus* (numbers in figure as in text on pp. 390, 393, and 394).

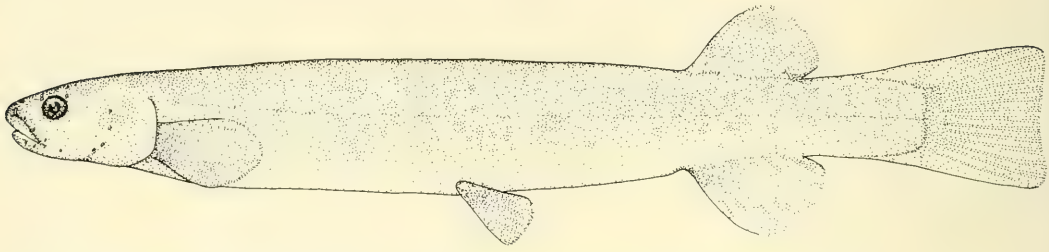


Figure 26. *Galaxias divergens* Stokell, 68 mm L.C.F., Mountain Camp Stream, Pelorus River System.

in head length, and usually fewer caudal and pelvic fin rays. The difference in jaw form immediately separates the two species.

Description. Trunk rounded to squarish in section, dorsally flattened with moderate development of a middorsal furrow, trunk profiles somewhat parallel, tapering anteriorly to a small head and becoming slender posteriorly. Caudal peduncle very long and generally slender, depth about half length. Lateral line an inconspicuous midlateral groove; accessory lateral line not observed. Head short, broader than deep, head depth conspicuously less than body depth. Eye small, towards upper head profile, and interorbital flat. Jaws equal or lower a little shorter, short in head length; cleft moderately oblique and reaching to about anterior eye margin; jaw profile from ventral aspect broad and shallow, somewhat flattened anteriorly. Jaws without canines, mesopterygoidal teeth weak; pyloric caeca lacking; gill rakers reduced to indefinite stubs.

Dorsal and anal fins small, somewhat fleshy at bases but membranous distally; short based and extending little beyond bases, distal margins rounded. Dorsal origin well forwards due to length of caudal peduncle, anal origin below or a little behind dorsal origin. Pelvic fin inserted at about midpoint of standard length; pelvic-anal interval moderately long, fin very short in interval. Pectoral fin inserted moderately high laterally; short in pectoral-pelvic interval, which is also rather short; distal margin of pectoral fin rounded, with middle rays longest. Caudal fin moderately long, emarginate, depth about equal to body depth; flanges of peduncle weak to moderate.

Variation. Meristic: dorsal 7 (9), 8 (58), 9 (34), 10 (10); caudal 13 (1), 14 (3), 15 (83), 16 (6); anal 8 (13), 9 (68), 10 (36), 11 (8); pelvic 6 (119), 7 (5); pectoral 9 (17), 10 (59), 11 (41), 12 (7); branchiostegals 6 (11), 7 (64), 8 (44), 9 (4); vertebrae 47 (2), 48 (14), 49 (38), 50 (69), 51 (81), 52 (44), 53 (2); gill rakers—these are so reduced and irregular in development that a satisfactory count was impossible. Morphometric: see Table 4, p. 387.

Coloration. Basic body color usually a striking creamy-white, covered dorsally and laterally with irregular, darker, greenish brown to gray vermiculations, which fail lateroventrally and ventrally. Head usually dark, pigmentation extending down on to cheeks. Less commonly the coloration consists of more diffuse, dark speckling.

Size. G. divergens is a small species, which is known to reach only 87 mm. Examples from the type locality were commonly over 70 mm, but those from other localities were generally smaller, usually 60–70 mm long.

Population differences. G. divergens has a moderately broad range in the North Island and the northwest of the South Island, and considerable differences between populations were observed. Stokell (1959b: 266) described *G. divergens* from a locality near Maruia Springs, noting that a form "from shingly streams in the Wellington Province agrees with *G. divergens*

Table 4. Morphometric variation in slender, alpine species (figures given as percentages of denominator of ratio).

	G. divergens			*G. paucispondylus*			*G. prognathus*		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./L.C.F.	85.5	87.7	90.9	84.8	86.2	88.5	86.2	88.5	90.1
B.D.V./S.L.	9.3	11.2	14.1	10.0	11.1	13.6	8.3	9.5	11.9
L.C.P./S.L.	14.7	17.0	18.9	16.8	19.0	21.4	15.3	16.7	18.0
D.C.P./L.C.P.	40.5	52.6	66.7	41.3	45.7	51.8	35.7	42.6	48.8
Pre D./S.L.	67.1	69.9	74.6	65.8	69.0	72.5	67.1	70.9	73.5
Pre D./Pre A.	94.3	98.0	102.0	94.3	97.1	101.0	93.5	95.2	98.0
D.F.B./S.L.	7.2	9.3	12.4	7.6	9.1	11.1	7.2	8.5	9.7
D.F.B./D.F.M.	51.8	61.7	76.9	54.4	62.5	80.0	57.5	64.9	75.7
A.F.B./S.L.	9.1	10.4	13.5	8.4	10.1	11.9	8.6	9.9	11.3
A.F.B./A.F.M.	59.5	68.5	78.7	55.6	64.5	72.5	61.0	70.4	78.7
Pre Pel./S.L.	47.6	50.5	52.9	43.9	47.4	50.5	48.1	50.8	53.2
Pec.Pel./S.L.	29.2	32.3	37.2	26.7	29.4	31.6	30.4	33.4	35.0
Pec./Pec.Pel.	29.6	39.6	48.4	37.9	46.6	54.4	28.6	35.7	42.1
Pel.An./S.L.	19.3	22.4	25.8	19.8	23.5	26.3	20.5	22.9	24.6
Pel./Pel.An.	34.4	45.1	54.2	37.5	45.6	55.6	33.8	39.2	43.8
H.L./S.L.	16.9	19.7	21.9	17.7	19.1	20.8	17.2	18.5	19.8
H.D./H.L.	41.0	49.3	54.6	39.2	48.1	59.5	40.0	44.8	52.6
H.W./H.L.	50.0	59.5	70.9	57.1	61.7	63.3	50.5	54.6	63.3
Sn.L./H.L.	25.6	29.3	33.3	26.5	29.4	34.6	25.0	28.7	31.7
P.O.H.L./H.L.	50.0	54.6	65.4	51.0	56.8	61.4	48.8	51.0	54.4
Io.W./H.L.	32.0	36.9	45.9	27.8	33.4	40.5	31.2	33.4	40.0
D.E./H.L.	16.0	18.2	21.3	12.2	15.0	18.7	12.8	14.1	16.7
L.U.J./H.L.	28.6	35.3	40.0	30.8	34.6	38.8	26.5	29.5	33.3
L.M./H.L.	26.2	31.2	36.0	28.1	30.2	35.1	30.6	32.9	35.6
W.G./H.L.	30.4	35.8	49.3	30.6	35.1	40.3	33.3	35.0	37.7
Fish examined		105			40			23	

in the number of ventral rays and the absence of pyloric caeca but has a head in length ratio of less than five, and a definitely curved mouth." He expressed the view that "the characters concerned are rather more important than come within the author's conception of subspecific distinction."

Populations of fishes like these are now known to be quite widespread. They do not seem to fall into more than one taxon and certainly form an assemblage that stands apart from the other species of the upland-alpine, slender-species group. The differences between the populations are decidedly less than differences between these *G. divergens*-type populations and other species in the species group. Accordingly, all these populations are included in a somewhat variable species, *G. divergens* Stokell.

Meristic characters were found to be similar in all populations and all characters examined. Maxima and minima in dorsal, anal, caudal, and pelvic fin ray counts in no case differed by more than one element between populations, and pectoral ray, branchiostegal, and vertebral counts by no more than two elements. Overlap between populations was thus found to be broad. Vertebral number and pectoral ray number showed slight general increase along a north-south axis (Fig. 27), although in both characters, one population or another was found to interrupt the continuity of the variation. The body proportions were found to exhibit greater variation. Fishes from the Mangatarere population were considerably stouter in build than other populations, this being evident in both the depth caudal peduncle/length of peduncle and body depth at vent/standard length ratios

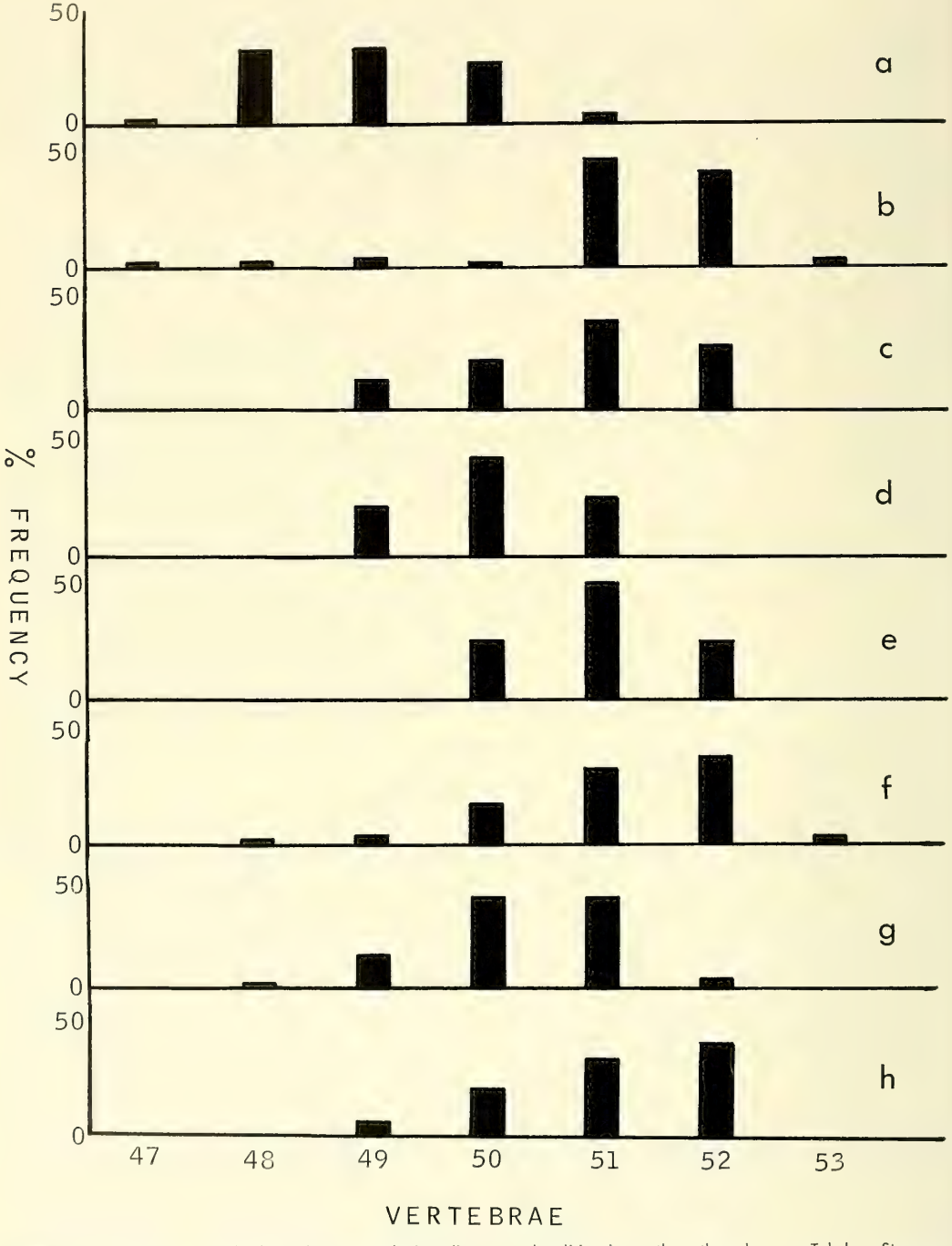


Figure 27. Variation in vertebral number in *Galaxias divergens*, localities in north-south order. a, Tukuhou Stream at Haromanga, Rangitaiki River System (54 examples); b, Hinaki Stream, Ruamahanga River System (74 examples); c, Mangakotukutuku Stream, Waikanae River System (54 examples); d, Hutt River (57 examples); e, Catchpool Stream, Wainuiomata River System (23 examples); f, Mountain Camp Stream, Pelorus River System (54 examples); g, Stream at Golden Downs, Matueka River System (68 examples); h, Maruia River, Buller River System (21 examples).

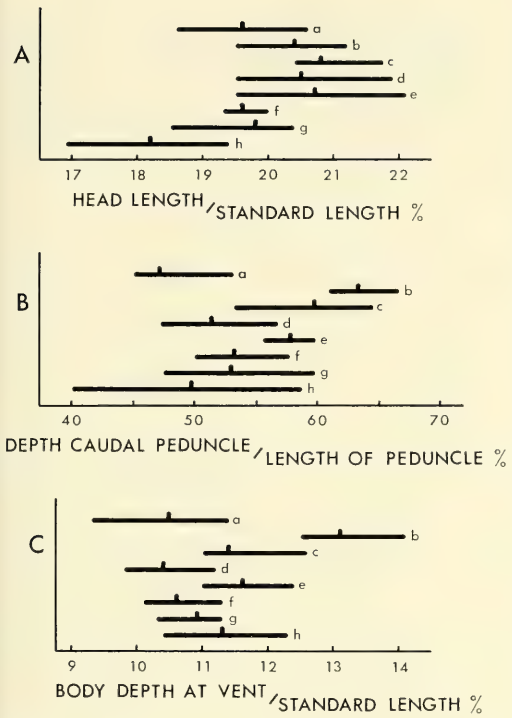


Figure 28. Variation in body proportions in *Galaxias divergens*, localities in north-south order. A, Head length/standard length ratio; B, Depth of caudal peduncle/length of caudal peduncle ratio; C, Body depth at vent/standard length ratio; a, Tukuhou Stream at Horomanga, Rangitaiki River System (20 examples); b, Hinaki Stream, Ruamahanga River System (13 examples); c, Mangakotukutuku Stream, Waikanae River System (9 examples); d, Hutt River (14 examples); e, Catchpool Stream, Wainuiomata River System (10 examples); f, Mountain Camp Stream, Pelorus River System (10 examples); g, Golden Downs Stream, Motueka River System (10 examples); h, Maruia River, Buller River System (17 examples).

(Fig. 28B, C). The Catchpool and Mangakotukutuku populations were also somewhat more stout than the others. Head length is less variable, except that the sample from the type locality, at Maruia, stands distinctly apart from all other populations (Fig. 28A). There is no obvious basis for this variability, and despite its extent, there appears to be only one taxon here, at the species level. Until the range of this species is thoroughly understood, it is not appropriate to name sub-species. It seems likely that many more localities for *G. divergens* within the known range, and particularly between those in the southern Wairarapa and the disjunct population at Horomanga, will be discovered. Data from these may make the inter-population variation more comprehensible.

Habitat. G. divergens is usually captured from small, moderately swiftly flowing headwater streams, which have gravel or boulder beds. Streams where *G. divergens* is abundant are usually stable, and often occur in narrow, steep gullies with little or no flood plain. The characteristic water type is turbulent but not broken; the fish characteristically live in the interstices of the stream substrate, and are almost always hidden.

Life history. G. divergens is restricted to fresh water and has been found only in flowing water, although a population is known in a tributary of Lake Rotoiti. Fishes collected from the Maruia, Golden Downs, Mountain Camp, and Catchpool populations in May were near maturity; others, taken in the Mangakotukutuku in September, the Catchpool and Hutt localities in November, and the Horomanga in December appeared to be mature. Adults in a large sample from the Mangatarere, collected in late February, were found to be spent, and the sample contained many small juveniles, mostly between 20 and 25 mm long. Recently hatched juveniles 10–12 mm long were collected from the Hutt River at Kaitoke in early February. These data suggest a rather extended spawning period in the spring and summer.

The eggs of *G. divergens* are of moderate size, 1.3–1.6 mm diameter, and very few in number, a female of 68 mm carrying 225 eggs. The breeding site is unknown to me. A search was made for the site when fishes were collected during December, when there were ripe fish in the population, and it was not discovered (G. A. Eldon, pers. comm.). Mature fish from the Horomanga locality exhibited a peculiar sex ratio, all the fish being females. The failure to find

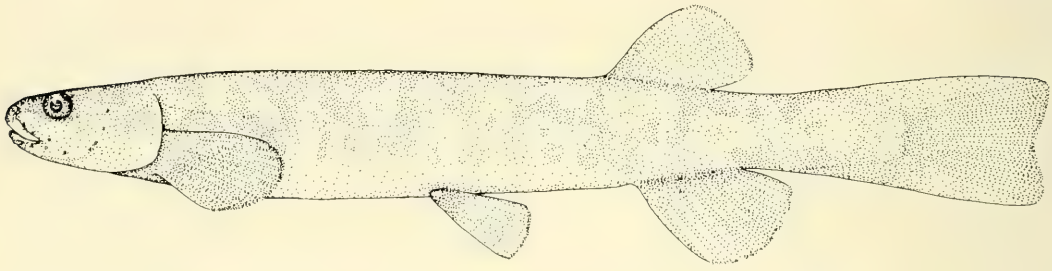


Figure 29. *Galaxias paucispondylus* Stokell, 70 mm L.C.F., Wilberforce River, Rakaia River System.

the spawning site may be related to a spawning migration in association with breeding, perhaps explaining the absence of males from the Horomanga sample.

Groups of juveniles may be found swimming freely in the still waters amongst rock piles at the edges of the pools and other places where there is very little flow.

Distribution. *G. divergens* is presently known over a broad area of the southern North Island and the northwest of the South Island. A single locality in the Bay of Plenty is known. *G. divergens* has been recorded from the following localities: Tukuhou Stream at Horomanga, Rangitaiki System (Fig. 25: 1*); a tributary of the Mangahao River at Mangamaire, Manawatu River System (2); Bull Stag Creek, Kiriwhakapapa tributary (3*) and Hinaki Stream, a tributary of the Mangatarere Stream (5*), both in the Ruamahanga River System; Mangakotukutuku Stream, Waikanae River System (4*); Hutt River at Kaitoke (6*); Catchpool Stream, Wainuiomata River System (7*); tributary of the Wakamarina Stream, Pelorus River System (8*); tributary of the Motueka River at Golden Downs (9*), and another tributary, the Clarke River at Hope Saddle (10); tributary of Lake Rotoiti (11*, Nelson Lakes); small tributary of Maruia River near Spring's Junction, upper Buller River (12*, type locality).

Galaxias paucispondylus Stokell, 1938
Figure 29

Galaxias paucispondylus Stokell, 1938: 203 (holotype: CMCNZ 73, seen; paratypes (10): CMCNZ 74, not seen; locality: Acheron River, tributary of the Rakaia River, Canterbury), 1949: 480.

Diagnosis. Differs from *G. divergens* Stokell (Fig. 26) in characters discussed in the diagnosis of that species (p. 384); differs from *G. prognathus* Stokell (Fig. 31) in having fewer anal fin rays, branchiostegals, vertebrae, and gill rakers. It also has a slightly stouter build, longer pectoral fins, and more anterior pelvic fin insertion, but these morphometric differences are rather minor. As with *G. divergens*, *G. paucispondylus* differs from *G. prognathus* chiefly in having sub-equal jaws, this character allowing immediate separation of the two species.

Description. Very elongate and slender bodied, trunk almost square in section, middorsal groove present, indistinct, dorsal and ventral trunk profiles about parallel, with belly somewhat deepened and rounded anterior to the pelvic fins especially in ripe adults; depressed anteriorly on head, somewhat compressed on caudal peduncle, which is very long and slender, much longer than deep. Lateral line a moderate midlateral furrow, accessory lateral line not observed. Head short and tapering, somewhat depressed. Eye small, upper margin near upper head profile, interorbital flat or slightly concave. Lower jaw a little shorter than upper, lips well developed; cleft of mouth extends to about anterior eye margin; profile of lower jaw from ventral aspect broad and shallow, somewhat flattened anteriorly. Canine teeth poorly developed or lacking in jaws; meso-

pterygoidal teeth rather poorly developed; gill rakers variable, weakly to moderately developed, often irregularly spaced with large gaps suggesting loss of rakers; pyloric caeca short.

Dorsal and anal fins somewhat fleshy at bases, short based; greatest fin length somewhat longer than base length, but fins not prominent. Dorsal fin insertion further forward in standard length than in most *Galaxias* (due to the great length of the caudal peduncle); anal origin usually a little behind dorsal origin. Pectoral fin quite small, rounded, inserted moderately high laterally. Pelvic fin short, inserted in front of midpoint of standard length. Caudal fin moderately long, truncated or slightly emarginate, fin depth about equal to greatest body depth, flanges of caudal peduncle moderately developed.

Variation. Meristic: dorsal 7 (3), 8 (10), 9 (36), 10 (9), 11 (1); caudal 15 (3), 16 (54), 17 (1); anal 7 (1), 8 (7), 9 (35), 10 (13), 11 (1); pelvic 6 (14), 7 (43), 8 (1); pectoral 10 (5), 11 (33), 12 (17), 13 (3); branchiostegals 5 (2), 6 (20), 7 (33), 8 (2); vertebrae 50 (2), 51 (10), 52 (18), 53 (9), 54 (1), 55 (0), 56 (1); gill rakers 1–5 (1), 1–6 (3), 1–7 (5), 1–8 (1), 2–6 (7), 2–7 (11), 2–8 (6), 2–9 (1), 3–7 (4), 3–8 (1). Morphometric: see Table 4, p. 387.

Coloration. The basic body color is a grayish cream, interrupted dorsally and laterally by usually bold greenish brown to gray vermiculations. These fail rather high laterally on the belly and caudal peduncle and do not extend much onto the fins except the caudal, which is often quite densely pigmented. The head is heavily pigmented dorsally and also laterally to just below the eyes, but the cheeks, ventral head, and belly are pale, virtually colorless. Quite commonly, this lack of pigmentation on the ventral trunk extends posteriorly beyond the anal fin, even as far as the caudal base. This is unusual in New Zealand galaxiids, in which the lateral trunk pigmentation usually extends as far down as the anal fin and covers the entire caudal peduncle.

Size. Stokell (1949: 480) recorded *G. paucispondylus* growing to 4.4 inches (112 mm). The largest examined in this study was 104 mm; *G. paucispondylus* commonly grows to 80–85 mm.

Population differences. Samples of *G. paucispondylus* studied came from a restricted area and only three distinct river systems. Samples from only two of these, the Rakaia and Ashburton, were of sufficient size to allow comparison, and the interpretation of inter-population differences is difficult without a series of populations. However, the more southern Stour (Ashburton) population was found to be generally more slender in form than that from the Harper-Avoca-Wilberforce Rivers (Rakaia). In the former, body depth at vent/standard length, head depth/head length, head width/head length, interorbital width/head length, and gape width/head length ratios are all lower (Fig. 30). The meristic data did not show recognizable differences between populations.

Habitat. G. paucispondylus occurs only in the swift, cold, snow-fed, boulder-gravel streams of sub-alpine and alpine Canterbury. These rivers tend to be unstable, flood severely with heavy rains and rapid snow thaws, and the rivers wind across broad, flat, open, gravel plains, flanked on either side by steep and often denuded, unstable hills. *G. paucispondylus* is characteristically found in these rivers in the moderately deep, broken-water riffles where the flow is extremely rapid.

Life history. G. paucispondylus is restricted to fresh water and has no juvenile whitebait stage. Ripe and spent adults were present together in samples collected in October, suggesting that spawning takes place in the southern spring. However, Stokell (1955: 32) reported that it occurs in March and April. It thus appears that *G. paucispondylus* may have prolonged breeding from spring through the summer to the autumn. The ovaries of fishes

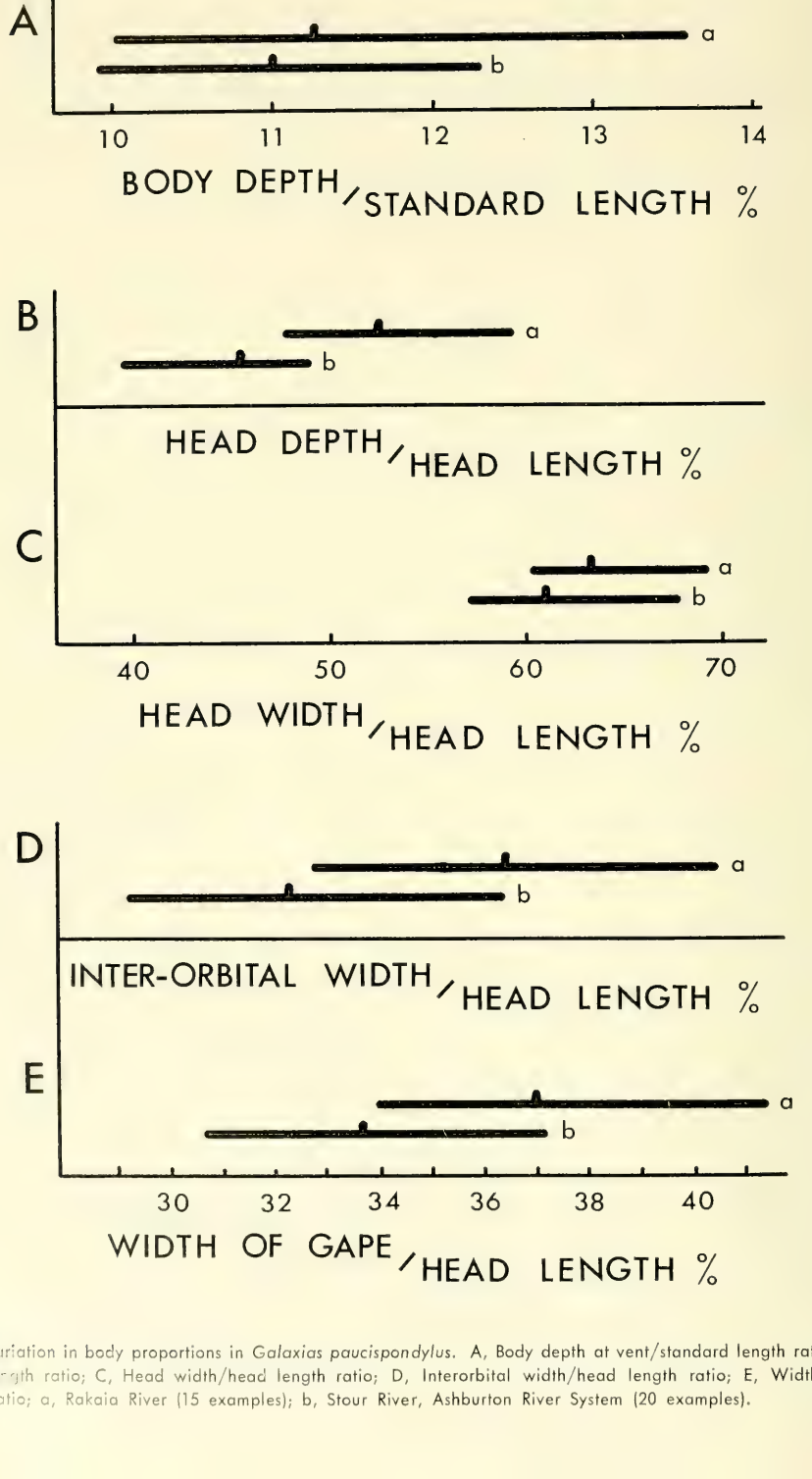


Figure 30. Variation in body proportions in *Galaxias paucispondylus*. A, Body depth at vent/standard length ratio; B, Head depth/head length ratio; C, Head width/head length ratio; D, Interorbital width/head length ratio; E, Width of gape/head length ratio; a, Rakaia River (15 examples); b, Stour River, Ashburton River System (20 examples).

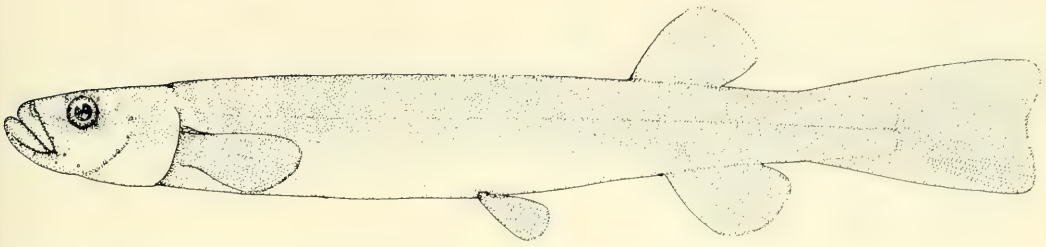


Figure 31. *Galaxias prognathus* Stokell, 64 mm L.C.F., Avoca River, Rakaia River System.

collected in June were in moderately advanced stages of maturation; others, collected in December, were invariably spent or had very immature ovaries.

The eggs of *G. paucispondylus* are very large, about 2 mm diameter when ripe. They are very few in number, a female 88 mm long having only 269 eggs. The breeding site is unknown to me and is undescribed, but is probably close to the normal adult habitat.

Distribution. G. paucispondylus is presently known only from upland and alpine Canterbury, on the eastern side of the Southern Alps. Populations are known at the following localities: Waimakariri River and its tributaries, the Cass and Porter Rivers (Fig. 25: 14); the Harper, Avoca, Wilberforce (15*), and Acheron Rivers (16) in the Rakaia River System; Stour River, Ashburton River System (17*); Deep Creek, a tributary of the Rangitata River at Mesopotamia Station (18*).

Galaxias prognathus Stokell, 1940
Figure 31

Galaxias prognathus Stokell, 1940: 422 (holotype: CMCNZ 75, seen; locality: Wilberforce River, Canterbury), 1949: 480.

Diagnosis. Differs from *G. divergens* Stokell (Fig. 26) and *G. paucispondylus* (Fig. 29) in characters discussed in the diagnoses of these species (pp. 384 and 390 respectively).

Description. Very elongate and slender in form, belly somewhat rounded and deepened in front of pelvic fins but tapering posteriorly to a slender caudal peduncle, which is very long and much longer than deep. Trunk flattened dorsally with a well-developed middorsal furrow. Lateral line a well-defined midlateral crease; accessory lateral line not observed. Head small and short, tapering considerably, and dorsally flattened; shallow, much broader than deep. Eye small, towards upper head profile, interorbital flat. Lower jaw much longer than upper, upper jaw short, and mouth upturned, lips prominent. Cleft of mouth oblique, usually not reaching anterior eye margin; lower jaw profile from ventral aspect broad and shallow, flattened anteriorly. Canine teeth lacking from jaws; mesopterygoidal teeth weak; gill rakers weak and irregular in development; pyloric caeca lacking.

Dorsal and anal fins showing some basal fleshiness, very short based; greatest fin length somewhat greater than basal length but fins not prominent; distal margin of fins rounded. Dorsal fin insertion well forward, anal origin below or a little behind dorsal origin. Pectoral fin very small and short, somewhat triangular, with the longest rays towards the upper edge of fin, inserted moderately high laterally. Pelvic fin also very small and short, inserted at about midpoint of standard length. Caudal fin moderately long, emarginate to slightly forked, fin depth about equal to body depth. Caudal peduncle flanges showing moderate development, extending about half-way along caudal peduncle to anal fin base.

Variation. Meristic: dorsal 8 (2), 9 (16), 10 (1), 11 (1); caudal 15 (1), 16 (17), 17

(2); anal 10 (13), 11 (7), 12 (1); pelvic 6 (2), 7 (18); pectoral 11 (3), 12 (16), 13 (1); branchiostegals 7 (14); 8 (6); vertebrae 54 (3), 55 (10), 56 (5), 57 (2); gill rakers 1–9 (1), 2–8 (4), 2–9 (9), 2–10 (1), 2–11 (1), 3–9 (1), 3–10 (3). Morphometric: see Table 4, p. 387.

Coloration. Similar to the two preceding species, pale creamish gray with bold, dark, greenish gray vermiculations dorsally and laterally. In a similar manner to the coloration of *G. paucispondylus,* the vermiculations fail rather high laterally, just below the eyes on the cheeks, and not far below the lateral line along the abdomen. The fins are largely colorless.

Size. G. prognathus is known to reach 79 mm length. Fishes 60–70 mm long formed a substantial proportion of a large sample from the Wilberforce River.

Population differences. Since adequate numbers of *G. prognathus* were collected from only one locality, and since all the samples were from the Rakaia River System, no meaningful comparisons of inter-population variation were possible.

Habitat. Like *G. paucispondylus, G. prognathus* occurs in alpine boulder-gravel streams and rivers, and the two species are sometimes taken from the same water. Generally, *G. prognathus* occurs in shallower, turbulent but not broken water. Stokell (1949: 480) reported having collected it mostly in situations where "a side stream rejoins the main stream at such a gradient that the water percolates through the boulders, leaving their upper surfaces dry." In the Wilberforce River, where *G. prognathus* was found to be quite common, the fishes were collected in "shallow riffles up to four inches deep and not particularly fast, but not in the flats," the stream bed composed of "boulders, stones and gravel with considerable silt and sand" (G. A. Eldon, pers. comm.).

Life history. Samples of *G. prognathus* examined were all collected towards the end of October. These fish were mostly spent, although a few were ripe, indicating that spawning was about finished. The eggs are large, about 1.8 mm diameter, and very few in number, a ripe female 68 mm long, with full abdomen, containing only 93 eggs. It is almost certain that the life history is restricted to fresh water, probably in the vicinity of the normal adult habitat.

As was the case with *G. paucispondylus,* my observations are at variance with those of Stokell's (1940: 424, 1955: 34); he reported that spawning occurs in the autumn. However, Stokell's observations were based on a female taken in April with ova measuring only 1.16 mm diameter (1940: 424). My observation of ripe eggs measuring about 1.8 mm suggests that Stokell's fish were not mature. Spawning is probably later in the year than "late autumn or early winter" as suggested by Stokell, and seems likely to occur in the early spring.

Distribution. G. prognathus is known from alpine areas of the central South Island. I have seen samples from the Rakaia River System, the Harper, Avoca, and Wilberforce Rivers (Fig. 25: 15*), and the Maruia River, Upper Buller River System (13). Collections of fishes in the adjacent Waimakariri, Ashburton, and Rangitata Rivers have not contained *G. prognathus.*

NEOCHANNA GÜNTHER

Neochanna Günther, 1867: 306 (type species *Neochanna apoda* Günther, 1867, by original designation).

Diagnosis. Characters generally those of *Galaxias,* but with pelvic fins reduced or lacking; mesopterygoidal teeth reduced or lacking. Jaw teeth sometimes compressed and incisorlike, or conical, as in *Galaxias.* No supraethmoid or ventral ethmoid, vomer folded upwards in front of ethmoid cartilage, ascending processes of premaxillae more or less meeting tips of frontals. No epipleural ribs. Flanges of caudal peduncle very strongly developed, usually confluent anteriorly with dorsal and anal fins.

Figure 32. *Neochanna burrowsius* (Phillipps), 108 mm T.L., Gawler Downs, Hinds River System.

Key to Species of *Neochanna*

1. Pelvic fins present ..... *N. burrowsius* p. 395.
   Pelvic fins absent ..... 2.
2. Median fins long, 14–19 rays, D.C.P./L.C.P. 129.8–200.0% ..... *N. apoda* p. 398.
   Median fins shorter, 11–16 rays, D.C.P/L.C.P. 95.2–135.1% ..... *N. diversus* p. 402.

Neochanna burrowsius (Phillipps, 1926) Figure 32

Galaxias burrowsius Phillipps, 1926c: 531 (holotype: DMNZ 521, seen; paratype: DMNZ 4646, seen; locality: a drain on the farm of the late Mr. A. Burrows, West Oxford, Canterbury); Stokell, 1949: 481.
Galaxias burrowsii Phillipps, 1927a: 14, 1927b: 11; Stokell, 1938: 205.
Saxilaga burrowsius: Scott, 1936: 110, 1966: 250.
Paragalaxias burrowsii: Phillipps, 1940: 39.

Diagnosis. Differs from *N. apoda* Günther (Fig. 34) and *N. diversus* Stokell (Fig. 36) in the presence of pelvic fins, and of mesopterygoidal teeth in many examples; also in the shorter median fins and lower ray counts in these fins.

Taxonomy. N. burrowsius has previously been included in the genus *Galaxias,* or in *Saxilaga,* which has characters intermediate between *Galaxias* and *Neochanna.* In its general morphology, it is similar to *N. apoda* and *N. diversus,* but whereas these latter species have entirely lost the pelvic girdles and fins, they persist in *N. burrowsius.* It also often has a few weak mesopterygoidal teeth, whereas *Neochanna* is usually described as having none. (In one specimen of *N. diversus,* I found a single tooth on each mesopterygoid.) These three species have the appearance of a radiation within the Galaxiidae, comprising species adapted to temporary creeks and bogs, which are able to aestivate when these dry up. They look like a single phylogenetic lineage, and their osteology supports this.

Osteological examination has revealed characters that indicate close relationship. In the ethmoid region of the skull, the three neochannoid species have lost the supra-ethmoid and ventral ethmoid bones. The ascending processes of the premaxillae have become pushed back over the ethmoid cartilage to meet the anterior tips of the frontals, and the vomer seems to have been folded upwards in front of the massive ethmoid cartilage, above the tip of the parasphenoid. In *N. burrowsius* and *N. diversus,* but not in *N. apoda,* the tips of the ethmoid cartilage, which diverge over the vomer, each have small tubular ossifications. In none of the three species are there epipleural ribs, although all the New Zealand species of *Galaxias* have them. On the basis of these considerations, I include *G. burrowsius* Phillipps in the genus *Neochanna* Günther.

A minor nomenclatural problem exists in the spelling of the name *burrowsius.* In his original description, Phillipps (1926c: 531) named the species *G. burrowsius,* reporting that the fish was collected on the farm of a Mr. A. Burrows. In later papers (1927a, b, 1940), he has spelt the name *burrowsii.* Mr. Phillipps (pers. comm.) has kindly advised me that he intended to name the species for Mr. Burrows, and not because of its habit of aestivating in small pockets in mud. The Zoological Code of

Nomenclature is not firm in the formation of patronyms, only recommending (1964: 33, recommendation 31 A) that they should be formed by the addition of "i" to the personal name, if masculine. However, rules for the emendation of name spelling (p. 35, art. 32a) are such that the original spelling must be maintained unless it contravenes mandatory provisions on name formation, or there are obvious, inadvertent errors. Neither of these is the case, so the original spelling must stand. The specific patronym can be regarded as grammatically correct either as an adjective—the Burrows *Galaxias*—or as a noun in apposition.

Numerous attempts to collect *N. burrowsius* from localities listed by earlier workers (Phillipps, 1926c: 532, Stokell, 1949: 482) have failed. The type locality appears to have disappeared as a habitat for *N. burrowsius,* since no creeks or drains could be found at the locality at West Oxford, from which Phillipps first obtained the species (K. F. Maynard, pers. comm.). The present work is based on series collected from localities associated with the Hinds River.

In his description of *N. burrowsius,* Phillipps (1926c: 531) pointed out that teeth were present "only on pre-maxillaries, lower jaw and tongue." Stokell (1945: 129) noted that he had been unable to recollect *N. burrowsius* from the original locality but (1938: 205, 1949: 482) redescribed it from further, new localities. In the later of these papers, he pointed out that teeth may or may not occur on the mesopterygoids. Scott (1966: 250) questioned the correctness of identifying the forms having toothed mesopterygoids with *N. burrowsius.* Since the condition is variable and Phillipps described the species from only two specimens, and since the subsequent collections of fishes included in this species have all been made from a restricted area of Canterbury, there seems little doubt that Stokell's action is correct and that the "neochannoid" species present in swamps and drains in Canterbury Province, in the vicinities of Ashburton and Christchurch, is *N. burrowsius* (Phillipps).

Description. Trunk much elongated and cylindrical, flattened dorsally with a deep middorsal furrow, dorsal and ventral trunk profiles parallel; little depressed on head, compressed on caudal peduncle, which is of moderate length and depth. Lateral line indistinct anteriorly, becoming a well-defined furrow posteriorly; accessory lateral line present, but weakly developed. Head rounded and blunt, cylindrical. Eye very small, deep set in head, with interorbital convex. Jaws very short, about equal or lower a little shorter, cleft of mouth extends to about anterior eye margin; profile of lower jaw from ventral aspect somewhat deep and narrow, a broad U. Canine teeth lacking in jaws; mesopterygoidal teeth poorly developed and few in number, or lacking. Gill rakers short; pyloric caeca well developed.

Median fins short based and low, with well-developed basal fleshiness. Overall fin length little greater than basal length, distal margins of fins more or less straight and tending to become parallel with trunk axis. Predorsal length moderate, anal origin usually below or a little behind dorsal origin. Pectoral fin very short, rounded, inserted moderately high laterally; pelvic fins much reduced, inserted at about midpoint of standard length. Caudal fin short and much rounded, fin depth about equal to body depth; caudal peduncle flanges very strongly developed and extending forwards to the insertions of the dorsal and anal fins, more or less confluent with the posterior ends of their bases.

Variation. Meristic: dorsal 7 (1), 8 (11), 9 (14), 10 (5), 11 (3); caudal 11 (2), 12 (1), 13 (20), 14 (12); anal 8 (4), 9 (15), 10 (10), 11 (5), 12 (1); pelvic 4 (1), 5 (14); pectoral 10 (1), 11 (10), 12 (3); branchiostegals 5 (1), 6 (9), 7 (3); vertebrae 51 (2), 52 (6), 53 (16), 54 (7), 55 (1); gill rakers 2–9 (1), 2–10 (1), 3–8 (1),

Figure 33. Distribution of *Neochanna burrowsius*, *N. apoda*, and *N. diversus* (numbers in figure as in text pp. 398, 402, and 404).

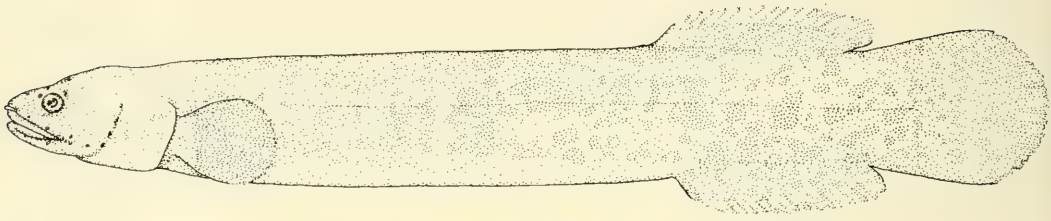


Figure 34. *Neochanna apoda* Günther, 110 mm T.L., tributary of Mangatarere Stream, Ruamahanga River System

3–9 (2), 3–10 (5), 3–11 (2), 3–12 (1), 4–9 (2), 4–10 (2), 4–11 (3). Morphometric: see Table 5, p. 399.

Coloration. Trunk a milky gray-brown, covered dorsally and laterally with fine, darker, greenish brown vermiculations, these extending well on to the fin bases. Belly paler, a milky brown.

Size. An example from the Anama sample measured 146 mm total length. Amongst the few fish examined, a good proportion were 100–125 mm long.

Population differences. Unfortunately, all the specimens examined were collected from the Hinds River System, in the same restricted area, so that no investigation of differences between populations was possible.

Habitat. N. burrowsius appears to be collected usually from small, muddy, or gravel-bed streams and creeks, often those draining swamps. Phillipps (1926c: 532) reported their ability to aestivate in small pockets of mud in the same manner as other *Neochanna* species are well known to do. Stokell (1949: 482) also reported specimens dug out of "damp earth and detritus at the bottom of a drain that had been dry for over a month."

Life history. N. burrowsius collected from the Hinds River System in early August were approaching maturity. All those taken in November were spent. Thus *N. burrowsius* probably spawns in the spring. No females from the August sample were sufficiently mature to permit egg counts or measurements, but egg number appeared to be moderately high, perhaps comparable with that of *G. maculatus.* There is no whitebait stage and no obvious juvenile-adult metamorphosis, and it is almost certain that *N. burrowsius* spends all its life in fresh water.

Distribution. N. burrowsius is known only from the Canterbury District, South Island. It has been collected from the following localities: West Oxford (Fig. 33: 27, type locality, Phillipps, 1926c: 532); Rangiora (28) and Tinwald (29, Stokell, 1949: 482); Gawler Downs, Anama District, Hinds River (30*).

Neochanna apoda Günther, 1867
Figure 34

Neochanna apoda Günther, 1867: 306 (holotype: BMNH 1965.11.5.8, not seen; locality: "near Hokitika," west coast, South Island); Hector, 1869: 402; Hutton, 1872: 61; Vollams, 1872: 456; Hutton, 1904: 51; Regan, 1905: 383; Phillipps, 1923: 62, 1926b: 297, 1927a: 14, 1940: 41; Stokell, 1949: 494.

Diagnosis. Differs from *N. burrowsius* (Phillipps) (Fig. 32) in characters discussed in the diagnosis of that species (p. 395); differs from *N. diversus* Stokell (Fig. 37) in having longer dorsal and anal fin bases, a much shorter caudal peduncle, a broader head, smaller eyes, and much longer jaws. It also has more rays in the dorsal and anal fins, more branchiostegals and, particularly in the southern part of its range, fewer vertebrae. *N. apoda* has much paler coloration than *N. diversus.*

Description. Trunk elongated and somewhat rounded, middorsal furrow prominent; dorsal and ventral trunk profiles about parallel; head little depressed anteriorly, caudal peduncle much compressed and thin posteriorly, short, much

Table 5. Morphometric variation in the "neochannoid" species (figures given as percentages of denominator of ratio).

	N. burrowsius			*N. apoda*			*N. diversus*		
	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.
S.L./T.L.	87.0	89.3	91.7	85.5	88.5	90.9	88.5	90.9	92.6
B.D.V./S.L.	10.0	11.0	11.9	10.4	12.9	14.9	10.5	11.9	15.0
L.C.P./S.L.	11.6	12.8	15.2	4.9	6.5	7.8	8.5	10.2	12.9
D.C.P./L.C.P.	56.8	64.9	76.9	129.9	158.7	200.0	95.2	11.2	13.5
Pre D./S.L.	69.4	73.5	76.3	69.9	72.5	75.8	71.4	74.1	76.9
Pre D./Pre A.	94.3	98.0	101.0	93.5	97.1	101.0	97.1	101.0	105.3
D.F.B./S.L.	9.7	11.6	14.0	19.3	21.9	25.3	10.1	13.8	16.3
D.F.B./D.F.M.	59.9	71.9	84.0	75.2	83.3	90.9	69.4	78.7	92.6
A.F.B./S.L.	10.5	13.1	15.8	20.2	22.4	25.8	16.7	18.9	20.8
A.F.B./A.F.M.	69.9	80.7	87.0	78.1	86.2	96.2	84.8	90.9	98.0
Pre Pel./S.L.	48.9	51.3	53.8	—	—	—	—	—	—
Pec.Pel./S.L.	29.0	34.0	36.1	—	—	—	—	—	—
Pec./Pec.Pel.	24.1	27.3	36.4	—	—	—	—	—	—
Pel.An./S.L.	20.3	23.6	27.1	—	—	—	—	—	—
Pel./Pel.An.	23.1	29.1	35.8	—	—	—	—	—	—
H.L./S.L.	16.7	18.4	20.2	18.5	21.2	24.2	18.6	20.1	21.8
H.D./H.L.	46.5	53.8	59.2	44.4	52.9	59.2	42.4	49.8	58.5
H.W./H.L.	52.1	59.5	64.1	56.8	62.9	71.9	53.8	59.9	65.8
Sn.L./H.L.	22.4	27.5	31.9	23.8	27.0	29.8	25.6	27.9	31.3
P.O.H.L./H.L.	54.6	59.5	63.3	57.1	63.7	70.4	58.8	62.9	68.5
Io.W./H.L.	32.8	36.1	40.0	32.6	36.8	42.7	35.5	39.1	45.1
D.E./H.L.	10.3	12.5	15.3	8.3	11.2	15.5	11.1	13.0	15.6
L.U.J./H.L.	27.6	31.3	33.3	36.2	39.7	44.1	27.0	30.4	32.3
L.M./H.L.	28.0	30.7	35.1	34.7	38.8	43.1	30.0	31.6	32.3
W.G./H.L.	34.5	38.0	42.4	36.1	41.7	50.0	30.8	35.2	38.3
Pec./H.L.	—	—	—	42.4	53.3	62.1	45.2	50.6	56.8
Fish examined		21			38			16	

deeper than long. Lateral line a deep lateral groove; accessory lateral line present. Head moderately long, broader than deep, somewhat bulbous behind nape, and tapering abruptly from just behind eye forwards on to a rather slender snout. Eye very small, deep set in head, with interorbital convex. Jaws about equal, very long, cleft extending well below eye, about as far as posterior eye margin. Gape very broad, profile of jaw from ventral aspect quite deep but moderately broad, somewhat flattened anteriorly. Canine teeth lacking from jaws; jaw teeth peculiarly compressed and incisorlike; mesopterygoidal teeth lacking; gill rakers moderate to short; pyloric caeca strongly developed.

Unpaired fins low, but very long based, with much basal fleshiness; greatest fin length little greater than basal length, distal margin of fin straight, parallel to trunk axis; fin bases confluent posteriorly with caudal peduncle flanges. Anal origin usually a little behind dorsal origin. Pectoral fin short, rounded, insertion high laterally. The fins all show coarse marginal serration.

Variation. Meristic: dorsal 14 (2), 15 (10), 16 (4), 17 (14), 18 (5), 19 (2); caudal 13 (1), 14 (5), 15 (11), 16 (16), 17 (3); anal 14 (2), 15 (6), 16 (9), 17 (10), 18 (4), 19 (6); pectoral 11 (2), 12 (15), 13 (20); branchiostegals 6 (12), 7 (19), 8 (5), 9 (1); vertebrae 52 (5), 53 (9), 54 (3), 55 (5), 56 (6), 57 (3), 58 (2), 59 (2); gill rakers 1–9 (1), 2–8 (18), 2–9 (12), 3–8 (7), 3–9 (4), 4–9 (1). Morphometric: see Table 5.

Coloration. Trunk usually sandy colored, darker dorsally, with the usual

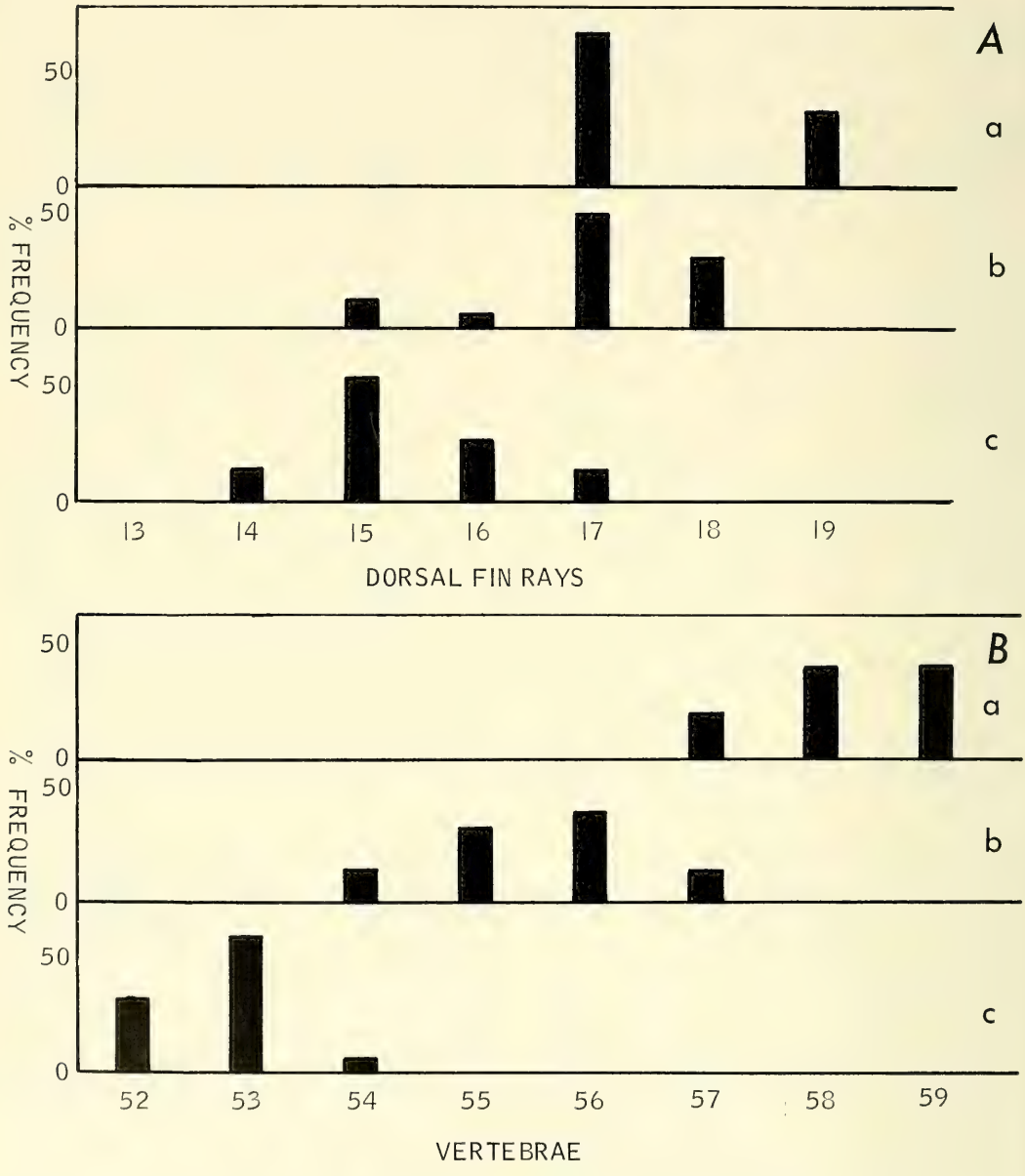


Figure 35. Variation in meristics in *Neochanna apoda*. A, Dorsal fin rays; B, Vertebrae; a, Wellington District (8 examples); b, Wairarapa District (20 examples); c, Western South Island—Westland District (13 examples).

irregular darker vermiculations of greenish brown color. Coloration much browner than most galaxiids in New Zealand, which are usually brownish gray to a deep purplish brown. Belly a pale cream-buff color. Fin bases well pigmented with vermiculations as on trunk. Samples from the west coast of the South Island were generally somewhat darker than northern ones, with the vermiculations tending to

become resolved into rather bold, broad, dark, vertical bands.

Size. Stokell (1949: 494) recorded *N. apoda* growing to 6.8 inches (173 mm). The largest example examined in the present study was 169 mm long. *N. apoda* appears commonly to reach 100–130 mm.

Population differences. N. apoda exhibits wide variation in meristic and some morphometric characters. Unfortunately, only two populations were available of sufficient size to allow adequate comparisons to be made. However, by grouping samples it was possible to compare data from three major, discrete areas. These were the Wairarapa, the Wellington Province west of the main ranges, and the west coast of the South Island. The number of specimens from the Wellington area (five) is totally inadequate for definitive comparisons, but these few specimens showed substantial, interesting differences from the others. Vertebral number was found to be greatest in Wellington fishes, somewhat lower in those from the Wairarapa, and minimal in those from the west coast of the South Island (Fig. 35B). Dorsal (Fig. 35A), anal, and caudal fin ray counts showed a similar trend; the greatest number of fin rays was found to occur in the more northerly populations. These data appear to be contrary to clines related to water temperatures, in which the populations in warmer areas would be expected to have fewer elements, unless there is something peculiar about the temperatures of water bodies from which these populations were collected. The variation in caudal fin rays is interesting in that this is otherwise by far the least variable of any of the meristic characters in the family. Branchiostegal number showed a different trend from other counts, being least in the Wairarapa samples and greatest in west coast samples, the Wellington fishes occupying an intermediate position.

The head length/standard length ratio of the Wellington fishes was much lower

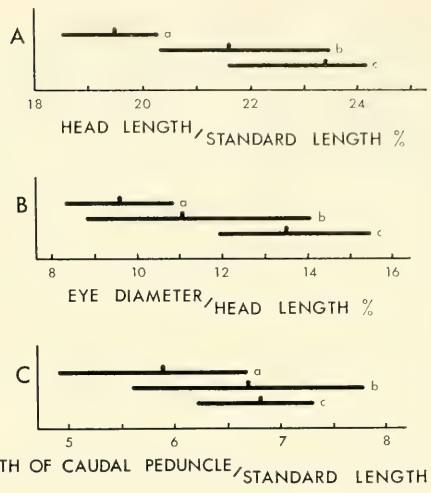


Figure 36. Variation in body proportions in *Neochanna apoda*. A, Head length/standard length ratio; B, Eye diameter/head length ratio; C, Length of caudal peduncle/standard length ratio; a, Wellington District (8 examples); b, Wairarapa District (23 examples); c, Western South Island—Westland District (8 examples).

than that of those from the Wairarapa, in which the ratio was lower than those from the west coast. Eye diameter exhibited similar variability. The length of the caudal peduncle was similar in Wairarapa and west coast material but greatly decreased in the few Wellington specimens examined (Fig. 36).

This variability appears to generate no clear pattern and it is obviously necessary to await collection of more material, especially from the western part of the Wellington province, before these differences can be understood. Eventually it may be necessary to divide what is here treated as a single species at either the species or sub-species level.

Habitat. In the Wairarapa, *N. apoda* has been usually collected in the upper reaches of small, spring-fed creeks, often filled with bottom-rooted vegetation. On the west coast of the South Island it was found in the tannin-stained waters of bush swamps, under a heavy forest cover, and in streams flowing into flax swamps. *N. apoda* is typical of the New Zealand mud-fishes in

its ability to withstand desiccation of its habitat. G. A. Eldon (pers. comm.) reported collecting one specimen from beneath a log in the middle of a partially cleared cow pasture, with no water near by at the time of capture. Phillipps (1923: 62) reported that it was collected from white pine swamps, and Reid (1886) reported that healthy *N. apoda* had been collected five or six feet down in clay, suggesting that the fishes follow moisture down holes left by rotted tree roots. Stokell (1955: 38) also mentioned its ability to bury itself in mud in times of drought.

Life history. Little is known of the life history of *N. apoda.* Stokell (1949: 495) noted that males taken in October "had the milt almost fully developed and appeared to be within a week or two of spawning." Davidson (n.d.) found that Wairarapa *N. apoda* spawn "probably . . . not before the end of November." A specimen taken in June by Phillipps (1926b: 297) is reported to have been in spawning condition. Material collected from the west coast of the South Island in late October was all apparently recently spent, or in the early stages of gonad rejuvenation, whilst the sample from the Kaipaitangata System (Wairarapa) collected in February contained a mixture of ripe and spent individuals. It appears that at present, no clear breeding period for *N. apoda* can be defined; it is possibly of long duration.

The eggs of *N. apoda* are moderately large, about 1.75 mm diameter, and few in number. A female from the Wairarapa, 115 mm long, contained only 533 eggs. Growth of juveniles is almost certainly in or near the adult habitat, as examples only 27 1/2 mm long were collected with adults. They are, at this small size, similar in form and coloration to the adults.

Distribution. N. apoda is found in the south of the North Island and on the west coast of the South Island. It is known from the following localities: Opunake (Fig. 33: 8); Feilding (9, Davidson, n.d.); Rangitikei (10, Phillipps, 1923: 62); Palmerston North (11, Stokell, 1949: 494); Rongotea (12*); Otaki (13*); Waikanae (14*); Masterton (15, Phillipps, 1926b: 297); tributary of the Kaipaitangata stream, Ruamahanga River System (16*); tributary of Lake Wairarapa at Pirinoa (17*); Oparara (18); Birchfield (19); Westport (20, Eldon, 1968); Greymouth (21, Stokell, 1949: 494); Kumara Junction (22*); Hokitika (23*); Ross (24, Eldon, 1968); Harihari (25*); Whataroa (26*).

Neochanna diversus Stokell, 1949
Figure 37

Neochanna diversus Stokell, 1949: 495 (holotype: CMCNZ 76, seen; locality: Kaitaia, North Auckland).

Diagnosis. Differs from *N. burrowsius* (Phillipps) (Fig. 32) and *N. apoda* Günther (Fig. 34) in characters noted in the diagnoses of these species (pp. 395 and 398 respectively).

Description. Rather slender bodied, trunk rounded in section without middorsal furrow; dorsal and ventral trunk profiles parallel from about head to dorsal origin, although the belly deepens noticeably in ripe adults. Trunk much compressed posteriorly on caudal peduncle, but little depressed anteriorly on head. Caudal peduncle deep and relatively long. Lateral line indistinct, accessory lateral line present. Head short, very blunt, broader than deep; head profile smooth and rounded, snout profile very convex. Eye very small, set deep in head, interorbital very convex. Jaws short, about equal, or lower protruding slightly; cleft of mouth reaching below anterior half of eye, oblique. Profile of jaw from ventral aspect rather broad and flattened anteriorly. Jaw teeth conical, lacking canines, usually no mesopterygoidal teeth, although one fish with one tooth on each mesopterygoid was observed. Gill rakers variable in length, from moderately to well developed; pyloric caeca also variable, usually moderately developed.

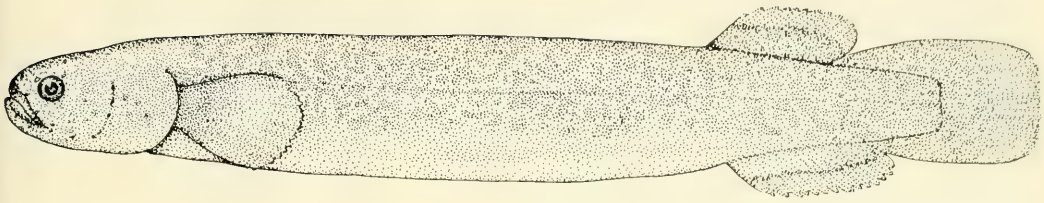


Figure 37. *Neochanna diversus* Stokell, 112 mm T.L., swamp at Waiharara, North Auckland District.

Median fins moderately long based and expansive, but extending little along caudal peduncle beyond end of fin base, extremely fleshy basally, fleshiness failing on distal half of fin, which is quite membranous; margins of fins straight, more or less parallel to trunk axis. Anal origin at or a little in advance of dorsal origin. Dorsal and anal fins confluent with caudal peduncle flanges, which are very strongly developed. Caudal fin short, moderately fleshy at base, truncated to rounded. Pectoral fin short, membranous or slightly fleshy, rounded, inserted high laterally. Margins of fins serrate.

Variation. Meristic: dorsal 10 (2), 11 (4), 12 (7), 13 (21), 14 (2); caudal 15 (6), 16 (25), 17 (5); anal 13 (4), 14 (5), 15 (19), 16 (4); pectoral 11 (1), 12 (14), 13 (17), 14 (4); branchiostegals 6 (12), 7 (24); vertebrae 55 (2), 56 (9), 57 (7), 58 (12), 59 (10), 60 (2); gill rakers 2–8 (5), 2–9 (3), 3–8 (8), 3–9 (14), 3–10 (6), 4–8 (2), 4–9 (3), 4–10 (1). Morphometric: see Table 5, p. 399.

Coloration. Dark colored; in populations examined from peat bogs, a dark smoky gray to almost black; profuse fine vermiculations cover the dorsal and lateral trunk and the fin bases. The belly is paler, smokey gray to somewhat rufous.

Size. An example from the Waiharara series measured 122 mm total length. Samples contained few examples more than 90 mm long.

Population differences. Noticeable differences in meristics were found for the two large samples of *N. diversus* examined. The Waiharara sample (the more northern locality) was found to have generally fewer counted structures, especially vertebrae, anal fin rays, and gill rakers. The sample from the most southern locality, Mount Pirongia, included only four fish, but these appeared to be more similar to those of the Waiharara series than to that from the Hikurangi swamp (e.g., vertebral number, Fig. 38). In the Waiharara and Hikurangi samples, ranges for anal fin rays and gill raker counts showed decided displacement from each other, and vertebral number was almost disjunct in the two samples (although the Hikurangi distribution is noticeably skewed). Thus, as was the case with *N. apoda*, differences between samples from highly isolated localities appear to be considerable. Collections of samples from further, intermediate localities and at-

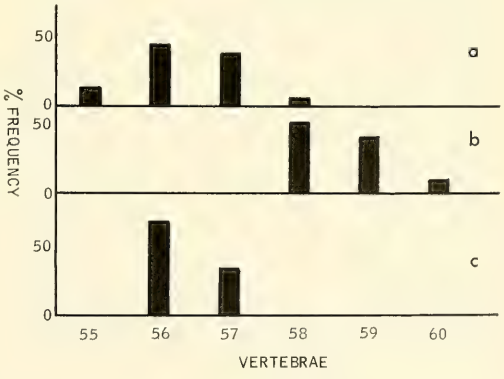


Figure 38. Variation in vertebral number in *Neochanna diversus*. a, Waiharara, North Auckland District (16 examples); b, Hikurangi, North Auckland District (22 examples); c, Mt. Pirongia, Waikato District (3 examples).

tempts to relate water temperatures or other ecological parameters to morphological characters may prove worthwhile.

Habitat. Stokell (1949: 495) discussed the habits of *N. diversus*, reporting that one of his specimens came from the mud of a creek in the summer, and that six were taken, free-swimming, during the winter. In March, 1965, several days were spent in the vicinities of Mt. Pirongia, Kaitaia, and Whangarei searching for this species in muddy creeks and drains, without success except at Mt. Pirongia. Only three specimens were found (the fourth was obtained from a local farmer). At Waiharara, one of the creeks searched unsuccessfully was a narrow channel draining a substantial shallow lagoon. Near this lagoon is a large area of Kauri-gum swamp, in which there are many small depressions, a few inches to several feet across and up to 18 inches deep. When examined, most of the holes were heavily overgrown with sphagnum, and often filled with twigs to the extent that they were scarcely distinguishable from the surrounding peat. It was here that *N. diversus* was found. By moving from hole to hole, clearing away the sphagnum and debris, waiting for the sediment to clear, and fishing in each with the electric fishing machine, it was found that each hole usually contained two or three fishes. Collections from the Hikurangi swamp, near Whangarei produced *N. diversus* from similar habitats. It appears, then, that these holes, rather than the streams running through swamps or draining them, are the characteristic habitat of *N. diversus*.

Life history. Mature, adult *N. diversus* were present in the samples collected from the North Auckland area in March. A single example from the vicinity of Waihi, collected in January, contained ovaries at an early stage of maturation. Stokell (1949: 495) found that examples collected from Kaitaia at the end of July were fully ripe or partly spent. These data indicate that *N. diversus* probably breeds during the winter. This is reasonable for a species that lives in a habitat that may dry up in the summer and that is known to be able to aestivate when this occurs.

The eggs of *N. diversus* are moderately large, those from the most mature female in the collection being about 1.6 mm diameter. These were not ripe; the fully ripe eggs may be somewhat larger. Corresponding with their size, they were found to be rather few in number, only 940 being present in a female 119 mm long.

Distribution. N. diversus was recorded by Stokell (1949: 495) from Waihopo (Fig. 33: 1), Kaitaia (3), and Mangawai (5). An example in the collection of the New Zealand Dominion Museum is from Waihi (6*); in the present study additional specimens were collected from Waiharara (2*); the Hikurangi Swamp at Whakapara (4*); Mt. Pirongia (7*). These localities suggest that it has a general distribution in swamplands in the Auckland Province, as far south as Waihi and Mt. Pirongia.

SPECIES *INCERTAE SEDIS*

Galaxias kaikorai Whitley

Galaxias kaikorai Whitley, 1956c: 34 (holotype: GMUO 6330–1; locality: Fraser's Gully, Kaikorai, near Dunedin, late Pliocene diatomaceous shale).

Taxonomy. Whitley applied this name to a fossil collected from a Pliocene freshwater deposit in southeastern New Zealand. Stokell (1945) examined this fossil thoroughly, concluding that it belongs in the genus *Galaxias*, but that it is probably not conspecific with living species. Whitley (1956) supplied no diagnostic characters for the species, and its validity is undetermined, but since the name was referred to a specimen and a partial description, the name has taxonomic standing. I have not examined the fossil and believe that further similar fossils have recently been discovered at the same locality (P. M. Johns, pers. comm.). Examination of these fossils may help to clarify the situation.

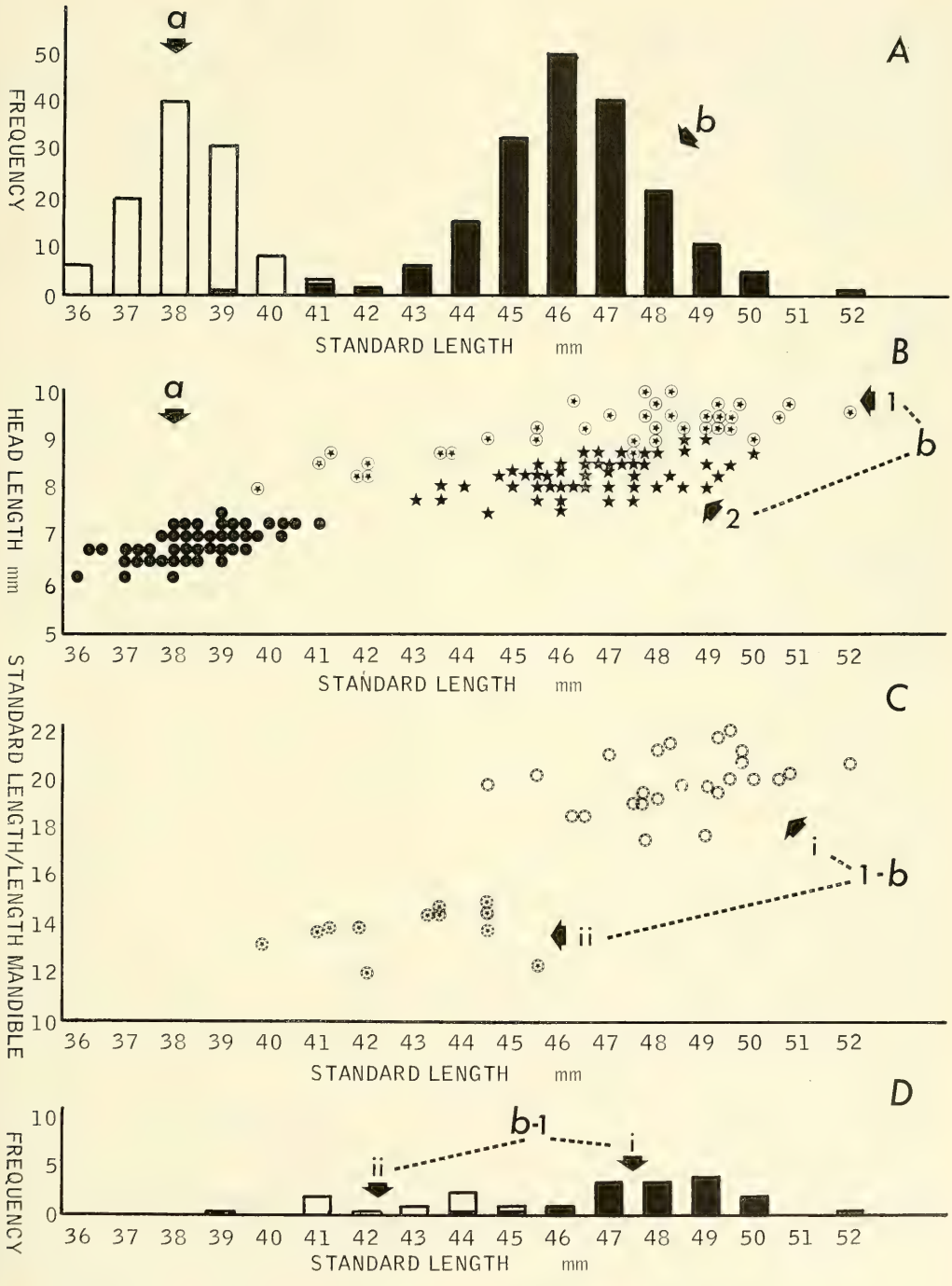


Figure 39. Identification of juveniles of diadromous New Zealand galaxiids (explanation of symbols in text, pp. 406–408).

Galaxias abbreviatus Clarke

Galaxias abbreviatus Clarke, 1899: 80.

Nomen nudum. This name was used by Clarke in a discussion of the *Galaxias* species of the west coast of the South Island. The origin of the name is unknown; it does not occur in earlier literature, and Clarke applied it to no description or type.

DISCUSSION

Identification of diadromous whitebait juveniles

The juveniles of the diadromous species of *Galaxias* in New Zealand lack many of the diagnostic characters of their respective adults, e.g., definitive pigmentation and dentition, and body proportions are very different from those of the adults. Overlapping meristic values for the five species also add to the difficulties of identification. Because of this, the species are difficult to distinguish (McDowall, 1964b: 142, 1965a). In my 1964 study, *G. fasciatus* and *G. postvectis* were not properly separated, and Woods (1966: 177) succeeded in identifying only three of the five species occurring in the rivers of the west coast of the South Island.

In New Zealand, *G. argenteus, G. fasciatus, G. postvectis, G. brevipinnis,* and *G. maculatus* have whitebait juveniles (McDowall, 1966a: 13). In earlier studies, samples were collected from the Buller River (Westland) and rivers nearby, and the four species, in addition to *G. maculatus,* were identified by rearing the fishes. The samples preserved at that time have been re-studied and the results are presented here.

The whitebait of *G. maculatus* (Fig. 40) is easily identified by its very bold pigmentation. The lateral line is very clearly defined by a series of large melanophores (which are small or lacking in other species), and there are several to many very large melanophores on the dorsal trunk anterior to the dorsal fin. In other species these melanophores are lacking. More objective characters that distinguish the whitebait of *G. maculatus* include its low pectoral fin ray number (11–15, usually 12–13), combined with high anal fin ray counts (14–18, usually 15–17).

After eliminating *G. maculatus* whitebait from samples, a length-frequency histogram of the remaining fishes showed that there were two very different size categories (Fig. 39A, a and b); these suggest size difference for some species at migration. A plot of standard length against head length indicated the same division of the samples (Fig. 39B, a and b). Further study of the fishes in the smaller size range (Fig. 39A, a) showed them to comprise only one species, and from much experience in collecting and studying these fishes, and having studied series of developmental stages from freshly migrated juveniles to fully pigmented sub-adults, I am quite confident that they are the whitebait of *G. fasciatus* (Fig. 41).

By elimination, the fishes in the larger size group (Fig. 39A, b) comprised a mixture of *G. argenteus, G. postvectis,* and *G. brevipinnis.* The adults of the first two species are much stouter than that of the third, and this difference is also evident in the juveniles. A plot of standard length against body depth at vent enabled division of the fishes into two somewhat overlapping groups, and the same division was produced in a plot of standard length against head length (Fig. 39B, b, 1–2). Examination of the fishes showed that the more slender ones (b, 2) also had a much shorter-based anal fin than the stout fishes, and that the anal fin origin was set further back from the dorsal origin. These two subjective characters enabled me to place the fishes in the overlap zone between the two major groupings, in the appropriate group. The slender fishes, from the slenderness, the short anal fin set back from the dorsal fin, and again from examination of developmental series, are the whitebait juveniles of *G. brevipinnis* (Fig. 42).

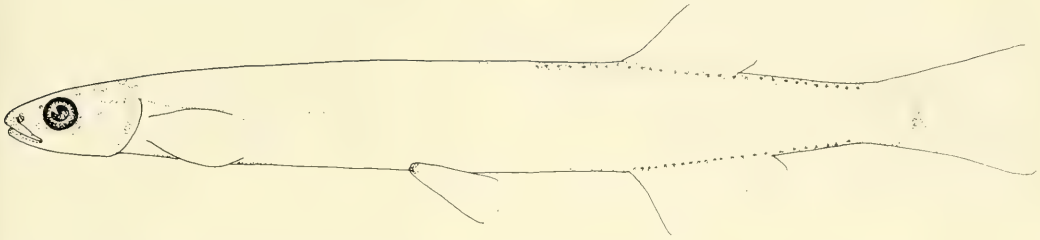


Figure 40. Whitebait juvenile of *Galaxias maculatus* (Jenyns), 53 mm L.C.F.

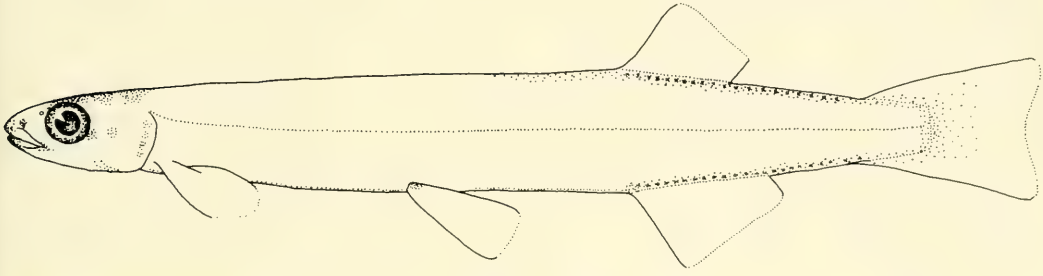


Figure 41. Whitebait juvenile of *Galaxias fasciatus* Gray, 48 mm L.C.F.

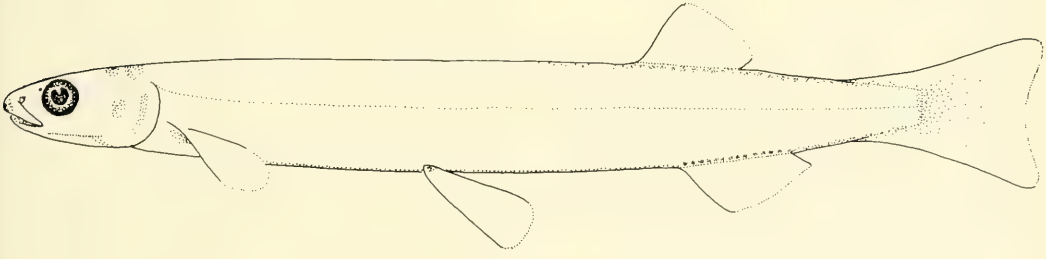


Figure 42. Whitebait juvenile of *Galaxias brevipinnis* Günther, 50 mm L.C.F.

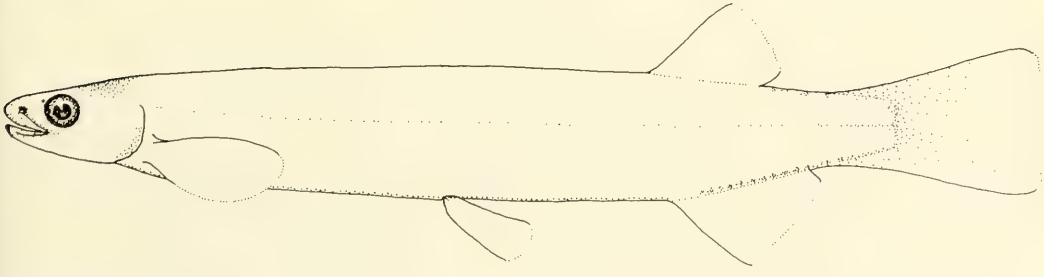


Figure 43. Whitebait juvenile of *Galaxias argenteus* (Gmelin), 50 mm L.C.F.

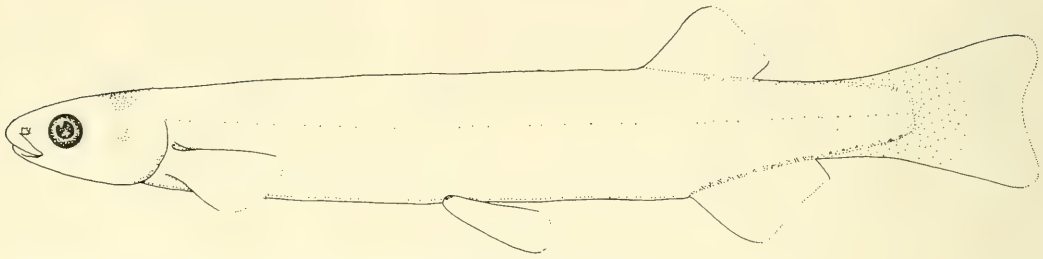


Figure 44. Whitebait juvenile of *Galaxias postvectis* Clarke, 54 mm L.C.F.

The remainder of the samples, containing the larger and stouter fishes, consisted of *G. argenteus* and *G. postvectis* (Fig. 39C), and these fishes could be separated on the basis of standard length (Fig. 39D). The adult of *G. postvectis* has a distinctly receding lower jaw, whereas in *G. argenteus* the jaws are about equal; this character enabled the identification of those fishes with the receding lower jaw as *G. postvectis* (Fig. 44), and the shorter ones with the lower jaw not receding, as *G. argenteus* (Fig. 43). I am fairly confident that the groups divided and identified by this procedure are correct, but the only way to confirm this appears to be further rearing trials.

This study has not isolated particular characters by which individual specimens of the four problematical species can be identified with any assurance. But it does show that it is possible to separate the species when they occur in mixed-species samples. In addition, the experience of carrying out this sorting procedure highlights the subjective characteristics of the whitebait of each species, and with this experience, it becomes possible to sort the species more directly. If this procedure can be carried out on a large scale, it will be possible to analyze seasonal differences in migratory patterns and the various ecological parameters which, in differing ways, influence the migrations of each of the species. Such an analysis would constitute significant progress towards understanding and intelligently managing the fishery.

In Table 6, the ratios for head length/standard length and body depth at vent/standard length of juveniles and adults of each of the five diadromous species in New Zealand are listed. These data show that in all the species, the head becomes proportionately much longer and the body

Table 6. Body proportions of diadromous galaxiidae.

		Head length as % of standard length			Body depth at vent as % of standard length			Fish examined
		Min.	Mean	Max.	Min.	Mean	Max.	
G. argenteus	Juvenile	19.6	20.0	21.2	11.9	12.8	14.0	6
	Adult	27.0	29.1	30.5	18.7	21.0	23.4	36
G. fasciatus	Juvenile	16.4	17.8	18.8	10.5	11.8	13.2	151
	Adult	22.8	25.9	28.6	15.0	17.9	21.4	60
G. postvectis	Juvenile	18.0	19.4	21.1	11.7	12.6	14.9	16
	Adult	21.2	23.0	25.0	16.4	19.6	22.4	25
G. brevipinnis	Juvenile	16.3	17.8	18.8	10.0	11.1	12.2	186
	Adult	20.6	23.6	28.7	11.0	13.2	15.3	160
G. maculatus	Juvenile	12.4	14.5	16.1	8.8	9.4	11.2	40
	Adult	18.5	20.0	21.6	10.3	11.6	12.9	40

deeper during growth. I have shown elsewhere (McDowall, 1968b) that in *G. maculatus*, the change in head length/standard length ratio is a result of trunk shrinkage just after migration, but I have insufficient material of the other species to determine whether this occurs in them also.

Life history and distribution patterns

Two distinct life history patterns are recognizable in the New Zealand Galaxiidae. Five species, *G. maculatus*, *G. brevipinnis*, *G. fasciatus*, *G. postvectis*, and *G. argenteus* have numerous, small to moderate-sized eggs, they spawn mostly in the autumn or early winter, and the freshly hatched larvae are carried to sea and undergo juvenile development there. About six months later, in the following spring, the slender, transparent whitebait juveniles, 40–55 mm long, migrate upstream in large, mixed-species shoals, undergo a minor metamorphosis, become pigmented, and assume adult form. In four of these species, the sub-adults become solitary in habit and are usually found in stream cover of some variety. The caudal fin changes from forked to emarginate or truncated, and all the fins become thick and fleshy, especially basally.

In contrast, the adult of *G. maculatus* retains the shoaling habits, the forked caudal, and membranous fins of the juvenile, and does not become secretive in habit. *G. maculatus*, which breeds in river estuaries on grass-covered, upper-tidal flats, differs from the other four diadromous species in its spawning habits. Although little is known about the spawning habits of these four species, they seem likely to breed in or near the adult habitats.

In some populations of *G. fasciatus*, and many of *G. brevipinnis*, the life cycle is restricted to fresh water. What changes have occurred in the life history of *G. fasciatus* subsequent to becoming landlocked in the Kaihoka lakes is presently unknown, but the population in Lake Okataina, and the many populations of *G. brevipinnis* in upland lakes, have a life history pattern in the lakes similar to the diadromous populations in the sea, although the juvenile life is of course lacustrine instead of marine.

Two small lacustrine species, *G. usitatus* and *G. gracilis*, are landlocked derivatives of *G. maculatus*. What is known of the life histories of these species suggests that they continue to spawn in the autumn, but that the diadromous habits have been eliminated. An Australian landlocked derivative of *G. maculatus* shows peculiar modification of the life history of the parental species, but this is not known to have occurred in these New Zealand species (see Pollard, 1966: 14).

The remaining seven New Zealand galaxiids have fewer, larger eggs, they spawn mostly in the winter and spring, complete their entire life histories in flowing, fresh water and do not appear to migrate. There is no whitebait stage in any of them, nor do they seem to exhibit any metamorphosis. How these species have been derived from the diadromous species is not obvious, but it seems likely that the easily dispersed diadromous species are ancestral to at least some of the entirely freshwater species.

New Zealand was heavily glaciated during the Pleistocene (See Fleming, 1962: 89), and the rivers must have been much colder than now. Species which were probably lowland or coastal during the glaciations must have become adapted to cold water and are now probably those found in upland-alpine areas, where temperatures are about as cold as they were coastally during the glaciations. By spawning in the spring, the young of these species develop and undergo early growth in somewhat less severe conditions than would be the case if they spawned in the autumn, as the diadromous species do. The possession of a marine migratory phase by the diadromous species may be an alternative strategy for surviving through the cold winter. Development in the sea gives them access to the prolific marine plankton, and in the

winter, the oceanic water temperatures during the glaciations would have been less extreme than river temperatures, making it worthwhile for the young fishes to spend the winter in the sea. The occurrence of five diadromous species in New Zealand and only three in warmer Australia perhaps supports this argument, and analysis of the life history patterns of South American Galaxiidae will be interesting, since *Galaxias* species occur in the far southern regions of Chile and Argentina.

The migratory stages of the Northern Hemisphere salmonoids appear to behave in a similar fashion. Kendall (1935: 11) noted that *Salvelinus* species in the far north are essentially marine species, entering fresh water occasionally for food and reproduction. Further south, "the marine forms gradually disappear, becoming almost or quite exclusively freshwater inhabitants at the southern end of each range." The presence of a marine migratory stage in both the salmonids and galaxiids may be connected with attempts to avoid the rigors of the extremely low temperatures and icing of freshwater habitats.

Egg number and egg size show good correlation with the alternative life history patterns. The species with marine life history stages have more numerous eggs, usually several thousand. High fecundity is perhaps related to high mortalities of larvae in the marine plankton and further mortality due to loss by dispersal in the sea and the hazards of making a migration from the sea into fresh water. Also related to increase in egg number, and the fact that the larvae enter the highly productive marine plankton, are the comparatively small eggs, with little yolk. The non-lacustrine species which are restricted to fresh water, in which mortality during the juvenile stages may be lower, and which don't suffer from dispersal by ocean currents (although they are carried downstream by river currents), have much fewer eggs, usually numbering only a few hundred. Increased survival of the fewer eggs is favored by larger size; this may be advantageous in rapidly flowing water in giving the freshly-hatched larvae a better chance of resisting downstream dispersal and also to compensate for any paucity of food available to very tiny fishes in rapidly flowing water. Greater yolk volume is advantageous because the larvae can depend on this for food for a longer period, and also because the larvae, hatching into swiftly flowing water, are larger and thus better fitted to maintain their position in the stream and find shelter from the currents.

Subjective observations indicate that the same relationship between egg size and egg number exists in the New Zealand Eleotridae. The species with fluviatile adults but marine or lacustrine juveniles—*Gobiomorphus huttoni* (Ogilby), *G. basalis* (Gray), *G. gobioides* (Valenciennes), and *Philypnodon hubbsi* (Stokell)—have much smaller and more numerous eggs than the single species which lives and breeds entirely in flowing, fresh water—*P. breviceps* Stokell.

This suggests that for diadromous species, high larval mortality due to predation and dispersal plus high food availability in a productive marine plankton have favored selection for numerous, small eggs. In contrast, in the non-migratory fluviatile species, somewhat lower larval losses due to less predation and dispersal, and greater ability to resist dispersal as a result of increased larval size at hatching, have favored selection for fewer, larger eggs, which carry more nutritive yolk.

There is a very clear relationship between life history patterns and range in the New Zealand Galaxiidae. It was previously pointed out (McDowall, 1966a: 16) that the fact that "certain species of *Galaxias* have marine whitebait is reflected in their New Zealand distribution." The present study, in altering the taxonomy of some problematical species, has further strengthened this observation. Reference to the

Table 7. Distribution of New Zealand Galaxiidae.

	Whitebait Juvenile	North of North Island	South of North Island	West Coast South Island	East Coast South Island	Offshore Islands	Localized
G. argenteus	X	X	X	X	x	X	–
G. fasciatus	X	X	X	X	x	X	–
G. postvectis	X	X	X	X	x	–	–
G. brevipinnis	X	X	X	X	X	X	–
G. maculatus	X	X	X	X	X	X	–
N. diversus	–	X	–	–	–	–	–
G. divergens	–	x	X	X	–	–	–
N. apoda	–	–	X	X	–	–	–
G. vulgaris	–	–	–	x	X	–	–
G. prognathus	–	–	–	x	x	–	–
G. paucispondylus	–	–	–	–	X	–	–
N. burrowsius	–	–	–	–	X	–	–
G. gracilis	–	–	–	–	–	–	X
G. usitatus	–	–	–	–	–	–	X

X = Present, widespread.
x = Present, restricted.
– = Not present.

species distribution maps (Figs. 7, 10, 20, 22, 25, 33) shows that the widespread species, and those which are found on the offshore islands, are the species which also have marine whitebait stages. *G. maculatus, G. brevipinnis, G. fasciatus, G. argenteus,* and *G. postvectis* have all been found over large areas, where suitable habitats have been searched, and various of these species have been recorded from the Cavalli, Chicken, Little Barrier, Mercury, Kapiti, Arapawa, D'Urville, Stewart, Chatham, Auckland, and Campbell Islands. *G. maculatus* is present in Australia, Tasmania, Lord Howe Island, New Zealand, and the Chatham Islands, Chile, Patagonia, and the Falkland Islands. There can be no question that the wide range of this species is entirely a result of the existence of the marine whitebait stage.

In marked contrast, the non-migratory species have a much more restricted range. The two main islands of New Zealand are divisible into four somewhat dubious, but presently useful, faunal regions. The North Island is divided centrally by the volcanic plateau, with large areas north and south of it. The areas east and west of the Southern Alps-Kaikoura Mountains mountain chain are separated by these high mountains. In Table 7, the New Zealand Galaxiidae are listed and their presence or absence in each of the four areas noted. This table illustrates dramatically the difference between the diadromous and non-migratory species in breadth of range. It also shows that the species in the latter group are restricted to one or two, occasionally three, of the so-called faunal regions. Two species have very localized distributions, occurring in only one water body. Five species occur solely in one area or extend marginally into a second; e.g., *G. prognathus* and *G. vulgaris* are found primarily to the east of the Southern Alps, but both species appear to have crossed the divide once, in the vicinity of the Lewis Pass, and have entered the upper reaches of the Buller River System, flowing to the west (see p. 424).

Two species occur widely in two faunal regions and one of these, *G. divergens,* is marginally present in a third. It should be noted that both these species are present primarily in the south of the North Island and the west of the South Island. Consideration of the range of some other animals, e.g., *Paranephrops planifrons,* the fresh water crayfish, suggests that the Buller-Nelson-West Coast area of the South Island has close biogeographic affinities with the south of the North Island. Fleming (1962) showed that for most of the Tertiary the two islands of New Zealand were connected across Cook Strait, and his map for the Pleistocene shows that the river systems from the Wellington area in the North Island and the northwest of the South Island were confluent in the now submerged area. The distribution patterns of *G. divergens* and *N. apoda* are thus easily explained in terms of land bridging of Cook Strait and indicate that these two areas have close faunal affinities.

Data on species range make it quite clear that the presence of a marine stage has resulted in a broad geographical range. This same factor, the presence of a marine stage in the life history, has also imposed some restriction on inland penetration and altitudinal range. Species that migrate up rivers from the sea are excluded from areas that the migratory juveniles are unable to reach in their migration. The extent of restriction in altitudinal range varies from species to species and is, in part, related to the climbing ability of each species. Climbing ability is, in turn, related to certain morphological adaptations (see "Adaptive radiation," p. 414). *G. maculatus* appears to be completely confined to lowland and coastal streams and rivers, and has been found to be virtually incapable of climbing a low artificial weir about six feet high across the Waikanae River (McDowall, 1964b: 145). Other diadromous species present in the river (*G. fasciatus, G. postvectis,* and *G. brevipinnis*) were found above the weir and were thus obviously climbing it. *G. brevipinnis* whitebait have also been observed climbing up the vertical concrete face at one end of an aqueduct beneath a road (K. F. Maynard, pers. comm.). *G. brevipinnis, G. argenteus, G. fasciatus,* and *G. postvectis* juveniles have been found to be extremely troublesome to keep in captivity because of their propensity for climbing out of aquaria. This ability is important to species migrating upstream from the sea, especially in a mountainous country like New Zealand; amongst the diadromous species, those which penetrate far inland, especially *G. brevipinnis,* are also good climbers.

The origin and age of the New Zealand galaxiid fauna

It is now fairly generally believed that the Galaxiidae, together with the Retropinnidae and Aplochitonidae, are derivatives of the primarily northern salmonoid fishes. The osteology of these three southern families suggests that they are probably derived from some very early osmeroid stock.[1]

The three families are restricted to the Southern Temperate Zone, except for a single, more tropical species in New Caledonia (this species is found only in cooler, mountain lakes). The northern salmonoid families which seem to have given rise to the southern families are found only in the Northern Temperate and sub-Arctic. Thus, this quite large and diverse group of fish families is confined to the temperate zones, exhibiting bipolarity at the subordinal level. They are cold water fishes and seem to be excluded from more tropical areas by temperature. If this is so, it is difficult to imagine how the southern families could have been derived from the northern families unless either there was a period in the early Tertiary when tempratures were considerably cooler than now, or southward dispersal took place by tropical submergence. Until the Pliocene cooling which led to the glacial periods, temperatures in the Tertiary are thought to have been warmer than now. Fleming (1962: 66) suggested that New Zealand was warmer than now during the late Mesozoic and remained warm well into the Tertiary. If, as suggested, the salmonoid fishes are limited in range by temperature, tropical submergence seems to be the most likely means of traversing the tropics. Hubbs (1953: 325) conjectured that the three southern families are "pre-Tertiary relicts of groups that failed to persist in the tropics." The basis for Hubbs's conclusion is not clear. Certainly none of the living generalized salmonoids are tropical, or even subtropical. Existing temperature limitations and inferred temperatures since the end of the Mesozoic suggest that occurrence of salmonoids in the tropics is unlikely at any time since the radiation that produced the southern salmonoid families occurred.

[1] The evidence on which this supposition is based is discussed elsewhere (McDowall, 1969; see also Weitzman, 1967).

Where the southern families entered the Southern Hemisphere is also not very clear. The existing predominance of the Galaxiidae, as well as the Retropinnidae, in the Australasian region suggests that dispersal occurred across the tropics in southeastern Asia. More than 20 galaxiids are recorded from Australia, 14 from New Zealand, 4–5 from South America, but only one from South Africa. These details suggest that South Africa is a most unlikely source of origin and dispersal, and that it is, rather, the end of a chain of dispersal areas, under the influence of the west wind drift. If South America were taken as the center of dispersal, and if we use existing currents (see Fell, 1967), then the Australasian fauna must then have been derived by dispersal eastwards via South Africa, and again, the presence of only one species there suggests the improbability of this having taken place. *G. maculatus* is present in Australia, New Zealand and South America, but not South Africa, and this suggests that it originated in Australia and spread eastwards. For such reasons, I think that Australia is the most likely area for the origin and dispersal of the family Galaxiidae, and that the New Zealand fauna was derived from the Australian one.

How the galaxiid fishes have dispersed is fairly clear, although the wide geographical range of the Galaxiidae has puzzled many ichthyologists and zoogeographers. As recently as 1950, Stokell discussed means by which the family could have dispersed by land routes. Long ago, however, Boulenger (1902: 84), noting that "most text books and papers discussing geographical distribution have made much of the range of a genus of small fishes, somewhat resembling trout, the *Galaxias*," pointed out that some species are not restricted to fresh water. I have earlier (McDowall, 1964a) analyzed the derivation of the New Zealand freshwater fish fauna, and at that time I concluded that since all the families in the fauna (including the Galaxiidae) contain species that have marine stages, their presence in New Zealand is simply and clearly explained by trans-oceanic dispersal. The existence of at least seven diadromous species of *Galaxias* (two in Australia, four in New Zealand, and one further species in both) strongly supports the hypothesis of oceanic dispersal, and the range of one of these species—*G. maculatus*—suggests that this dispersal continues (McDowall, 1966a). It appears that the East Australian current, which travels down the east coast of Australia and which may impinge on much of the west coast of New Zealand, supplies a suitable mechanism for dispersal from Australia to New Zealand (see Fell, 1962, 1967). However, it is uncertain how much this current affects the New Zealand region. Burling (1961: 51) suggested that the Tasman current, which flows on to the west coast of New Zealand, is derived from the East Australian current as it turns eastward towards the central Tasman Sea. The similarities between the marine faunas of southeast Australia and New Zealand (see Moreland, 1958, for fishes, and Fell, 1967, for evidence of recent dispersals) support the probability of water transport in this manner. However, Dr. B. V. Hamon (pers. comm.) suggested that eddies that break off from the East Australian current may be a mechanism by which water is carried across the southern Tasman Sea, but that at present there is no evidence to suggest that these eddies persist over such distances, and it is not known how long it would take such eddies to travel across.

Fleming (1962: 105) concluded that "during the early Cretaceous, the geanticline west of the New Zealand geosyncline could have extended north to New Caledonia," but "at no time is there any evidence for direct trans-Tasman connection with Australia." There seems little likelihood of a suitable land bridge between New Zealand and Australia. In 1963 (p. 382) Fleming pointed out that if "the podocarps, *Sphenodon*, the frog *Leiopelma*,

many invertebrates, *Nothofagus*, and perhaps the ratite birds walked into New Zealand . . . . across an Antarctic land bridge from South America lasting at least into the middle Cretaceous, we are left with problems almost as great as those solved. What kept the land dinosaurs, the early mammals and snakes from New Zealand?" On this basis, he gave "wavering support to the view that the dispersal of the Paleoaustral organisms, like that of the Neoaustral element, was across the sea." The whole idea of land-bridge dispersal of the Galaxiidae to New Zealand must be discarded; or looking at the problem from a different perspective, the present range of galaxiid fish gives absolutely no support for any land connection between New Zealand and any other land area at any time.

The age of the New Zealand galaxiid fauna is uncertain. The comparative sizes of the families of freshwater fishes in the New Zealand fauna (and none of them looks like a relict)—Geotridae, one species; Galaxiidae, 14 species; Retropinnidae, six species; Aplochitonidae, one species; Anguillidae, two species; Eleotridae, six species; Cheimarrichthyidae, one species —suggest that the Galaxiidae may form the oldest existing element in the freshwater fish fauna. The fossil record is of little help in dating the fauna, since the only galaxiid fossils are from the Upper Pliocene of Fraser's Gully, Kaikorai near Dunedin. No other fossils of any freshwater fishes are described from New Zealand, and no galaxiids are recorded from other regions. Romer (1966: 356) listed a *Galaxias* from the Oligocene of New Zealand, but the original record of this fossil is unknown to me in any galaxiid literature. The Oligocene of New Zealand was a period of extreme marine transgression, and there was very little emergent land (see Fleming, 1962: 74); freshwater deposits would be very limited in extent, if present.

The fossil record thus provides little information on the age of the family, or on how long it has existed in New Zealand. The number of species in New Zealand, and their distribution pattern, suggests initial arrival in the early or mid-Tertiary, certainly considerably before the period of the Fraser's Gully deposit. Romer (1966: 355) recorded salmonoid fishes back to the Upper Cretaceous, and one existing genus—*Thymallus*—in the Eocene. Osmeroid fishes from which the southern families seem to be derived are dated back to the Miocene. The prospect that the salmonoid fishes were present in the Australasian region as long ago as the beginning of the Tertiary must be recognized.

Adaptive radiation

Since the family Galaxiidae is by far the largest family of freshwater fishes in New Zealand, it probably represents an old element in the fauna. However, to what extent the present fauna represents the fauna of the Tertiary is not clear, and it may be that as a result of changes in land form, marine transgressions, and glaciations during and after the Tertiary, the present fauna is only a surviving remnant of a more extensive fauna. But there are no apparent relicts in the fauna. If the neochannoid species represent a distinct radiation, independent of the Tasmanian mudfishes, they would seem to constitute an old element in the fauna, but the distribution of the three New Zealand neochannoid species seems to be a result of obvious geological events, like the rise of the South Island mountain chains and the central North Island volcanic plateau, or the marine transgressions of the earlier Tertiary. If these are old species, they give no indication of significant extinction.

All the New Zealand freshwater fishes fall into species groups (or are the sole representatives of their family in New Zealand). And those species that have no close relatives in the New Zealand fauna have such relatives in Australia. The relationships and distribution patterns of the New Zealand freshwater fishes give no

evidence for the occurrence of much extinction, and most appear to be rather recent in origin. Apart from man-caused extinction, I see no reason to suspect that the New Zealand freshwater fish fauna, including the Galaxiidae, has ever been any more diverse or speciose than it is at present.

The galaxiid fauna has been built up in two ways—by invasion from Australia and by speciation in New Zealand. As I discuss in the section "Species groups and phylogeny" (p. 418), I think that invasion has played an extremely important role in the development of the fauna, and I think that evolution of the fauna in the New Zealand region has been slow and rather ineffective in populating New Zealand's fresh waters.

There is little question that the fauna is depauperate. Comparison of New Zealand's freshwater fish fauna, comprising about 31 species, with that of Japan, 127 species (Okada, 1960), or the British Isles, 72 species (Regan, 1911), suggests that the freshwater habitats of New Zealand are far from saturated and that there is considerable scope for invasion. (This is not meant to imply that potentiality exists for the introduction of game fishes, since the past results of such introductions to New Zealand indicate that they may have serious effects on the existing fauna (McDowall, 1968a).) It is not surprising that the fauna is depauperate. New Zealand has been geographically isolated from other land since at least the end of the Mesozoic (Fleming, 1962: 105), and this has completely prevented the invasion of New Zealand by primary or secondary freshwater fishes. What is interesting is the failure of the species arriving to radiate in the semi-vacant and highly productive freshwater habitats of New Zealand. I find it surprising that so much of the fauna is adventive and not a result of diversification of stocks in the New Zealand region.

There are no herbivores in the New Zealand freshwater fish fauna. This is almost certainly a result of the scarcity of aquatic vegetation, which is itself at least partly related to the mountainous character of many New Zealand rivers. Furthermore, none of the species can be classed as piscivorous, data showing that some species may occasionally take fish, but that it is not customary (McDowall, 1965b, 1968b, Hopkins, 1965). Stream invertebrates make up the bulk of the food of all species, except for very large examples of the long finned eel, *Anguilla dieffenbachii* (Cairns, 1942: 139).

Galaxiids have invaded a wide variety of habitat types. Rapid-water species tend to be more slender in form, but are, in their general characters, similar to slack-water species. A few, e.g., *G. brevipinnis, G. postvectis,* have a receding lower jaw, which suggests adaptation to feeding off the stream bottom. Conversely, *G. prognathus* has a conspicuously protruding lower jaw, and this is a very obvious adaptation for picking invertebrates off the under sides of rocks. There is some variation in dentition, but only in the degree of development of lateral canine teeth in the jaws and of mesopterygoidal teeth in the roof of the mouth.

Most species are solitary and secretive. They are usually found in heavy cover and have great thickening of the fins, which provides resistance to fin damage when the fish swim amongst rocks and logs; these species also almost invariably have emarginate to truncated caudal fins. The pectoral fins are usually placed low latero-ventrally on the trunk, a modification probably related to bottom resting and feeding habits. *G. brevipinnis,* in which this is most pronounced, also has deep corrugations on the lower surfaces of the pectoral fins, which may help the fish to grip the stream bottom and maintain its position in the very rapid flow of its habitat. In contrast, the few species that shoal and live openly in pools have more membranous fins, the pectorals are positioned much higher laterally on the trunk, and the caudal has a definite fork. It seems justi-

fiable to interpret these characters as being related to the shoaling or midwater habits. The functional nature of the differences is perhaps least obvious in the caudal fin, although in shoaling groups, e.g., clupeids, the caudal fin is invariably forked, whilst in secretive, cover-dwelling groups, e.g., umbrids, the caudal fin tends to be truncated or rounded. Furthermore, the juveniles of the diadromous species are shoaling in habit and have forked caudal fins, the fins only becoming emarginate as the fishes mature and become solitary and seek cover. A further character related to shoaling habits, and also characteristic of shoaling fishes in general, is silvery coloration on the abdomen, present in the New Zealand Galaxiidae only in *G. maculatus* and its shoaling derivatives.

The low position of the thick, fleshy pectoral fins has served as a preadaptation for climbing. The diadromous species, which have the pectoral fins inserted low on the lateroventral trunk are much better climbers than *G. maculatus*, in which the fins are higher. The fact that the pectoral and pelvic fins are about flush with the ventral trunk and have the lamina facing downwards seems very important in the great climbing ability of species like *G. brevipinnis, G. fasciatus,* and *G. postvectis.*

The differences between the diadromous and freshwater species in egg size and number is discussed in the section on life history patterns (p. 409). A further difference between these groups of species is the length of the gill rakers. The five diadromous species and two lacustrine species (*G. usitatus* and *G. gracilis*) have long, well-developed gill rakers, whereas most other species have much shorter, sometimes irregularly-spaced rakers. The tendency towards gill raker reduction is especially evident in the slender alpine species, *G. divergens* and *G. prognathus.* These differences correlate with the existence of a shoaling, plankton-feeding phase in those species with long rakers and the lack of such a phase in the fluviatile species.

One of the most distinctive character divergences in the New Zealand Galaxiidae is the probably neotenic retention of shoaling habits and the associated morphological peculiarities seen in *G. maculatus.* It is notable, though, that this apparently did not originate in the New Zealand region, but its presence in New Zealand represents an independent invasion from Australia.

The three neochannoid species have not hitherto been discussed in relationship to the radiation of the family. This is largely because their adaptations represent a radiation into the most peculiar niche occupied by members of the family in New Zealand, though this group, too, might have originated in Australia and dispersed to New Zealand. If not, these species represent the most striking example of inventiveness in the New Zealand galaxiid fauna. There are three species that occur in swamps, swampy creeks, and sometimes springs, and that have an ability to aestivate during droughts. Common morphological characters, like loss or reduction of the pelvic fins, reduced eyes, long nostrils, low median fins that are more or less confluent with the caudal fin, rounded caudal fin, are interpreted as modifications for a semi-burrowing existence.

The limited extent of the radiation of the New Zealand Galaxiidae suggests that they are a conservative group. In this they are similar to their Northern Hemisphere relatives—the Salmonidae and Osmeridae—which are principally cold water predators of rather uniform morphology, although their habits may vary. The differences that have developed in the Galaxiidae are usually variations on the theme of solitary, secretive invertebrate predators. The most persistent variation involves adaptations to different water types—placid pools in stable bush streams to rushing torrents in open, unstable shingle rivers—and the persistence or loss of the marine whitebait juvenile stage. In the case of habitat differences, morphology shows little variation

—usually some elongation and depression in rapid-water species. The only obvious differences associated with the presence or absence of a whitebait stage are those related to survival of the progeny (egg size and number) and feeding (length of gill rakers). These characters are those likely to be most affected by selection, since the low saturation of the New Zealand freshwater habitat leads to little interspecific competition—selection is mostly intraspecific and related to feeding and reproductive efficiency.

The conservativeness of the group is seen in its failure to become open living and benthic, like the eleotrids, which are almost certainly more recent invaders. They have not become mid-water pool-living species like the species of *Retropinna*, but instead, when found in pools, generally skulk in marginal cover. They have mostly been unable to remain in streams that have lost their forest cover, and except in localities that may have been naturally alpine grassland in Central Otago and alpine Canterbury, streams without cover are mostly populated by eleotrids, eels, and sometimes *Retropinna*. Nor have they been particularly successful as lacustrine species. *G. argenteus* and *G. fasciatus* are known as adults from very few lakes; *G. brevipinnis*, although commonly found in lakes in the juvenile stages, is rarely lacustrine as an adult.

The exception to all these is *G. maculatus* and its derivatives. They are shoaling, open-living, pool-dwelling species, which have persisted in streams without cover and have become partly lacustrine. But apart from the landlocking in *G. usitatus* and *G. gracilis*, these characteristics do not represent evolution in the New Zealand region but are a product of dispersal of *G. maculatus* from Australia. The dominating impression acquired from studying the New Zealand Galaxiidae is that they have adapted their basic structure and way of life to a variety of water conditions, and have pursued their invertebrate-feeding habits in these.

Analysis of sympatry in the family in New Zealand shows that there is likely to be little interspecific competition. *G. usitatus*, *G. gracilis*, *Neochanna diversus*, and *N. apoda* have never been collected from the same water bodies as other galaxiids. This is also true for most of the range of *G. divergens*, but this species is known to be sympatric with *G. prognathus*, *G. vulgaris*, and *G. brevipinnis* in two localities. *G. vulgaris* is found in some waters with *G. brevipinnis* below some of the South Island alpine lakes and with *G. paucispondylus*, *G. prognathus*, and *N. burrowsius* in a few Canterbury rivers.

The species that exhibit broad sympatry are the diadromous species—*G. maculatus*, *G. brevipinnis*, *G. argenteus*, *G. fasciatus*, and *G. postvectis*—plus *G. prognathus* and *G. paucispondylus*, both of which are known from very few rivers, and occur together and with *G. vulgaris*, *G. brevipinnis*, or *G. divergens*. There is a likelihood here of competitive species interactions, and in these species there are some signs of significant niche differences; this is a profitable area for further study.

The sympatry of the diadromous species is interesting in that these species appear to be a product of successive invasions of the New Zealand region. All five species probably occur together in mixed associations as juveniles in the sea, and they migrate upstream from the sea together (McDowall, 1966a). It is unusual, however, for the adults to be taken from precisely the same habitat type, even though several species may be present in the same pool-rapid series in just a few yards of stream. The habitats of *G. fasciatus* and *G. argenteus* are especially similar, but the common association of these species in nature suggests that some habitat divergence is likely. A detailed study of microdistribution in river systems where various of the species are sympatric may provide interesting data

on niche and the effects of sympatry on niche breadth.

Species groups and phylogeny

The New Zealand Galaxiidae are easily divided into a series of small, distinct, species groups. These vary in their compactness, but they combine species that appear phylogenetically more closely related to each other than any species in one group is related to those in other groups. Although it is possible to list characters that unify the species groups, many of these are adaptive. However, the general form and habits of the species in these groups show such similarities that they seem to be valid. The species groups are as well defined by the gaps between species groups as by the similarities between the contained species.

There is a group of small, slender species that are somewhat compressed in form and have membranous fins, a long-based anal (Fig. 45, B, f, g, h), a forked caudal, and shoaling habits. They vary somewhat in their reproductive cycle, but otherwise form a compact group. *G. maculatus* (Fig. 21) is one of the more distinctive New Zealand *Galaxias* species, and probably stands far apart from other New Zealand species, except its immediate derivatives. The fact that *G. maculatus* is present in Australia, Tasmania, New Zealand, the Chatham Islands, South America, and the Falkland Islands has important implications in an analysis of the phylogeny of the family in New Zealand. The only way this species could have attained its present distribution is by trans-oceanic dispersal. Existing ocean currents indicate that *G. maculatus* probably originated in Australia and dispersed eastwards, in the west wind drift. If this is so, then *G. maculatus* has no direct affinities with other New Zealand species groups. Since populations from these widely separated land areas are conspecific (Stokell, 1966: 76, McDowall, 1967b) it seems that the original dispersal occurred quite recently.

Comparison of *G. maculatus* with *G. usitatus* and *G. gracilis* (see McDowall, 1967a: 3) shows that the latter two species, each of which is confined to one small lake, are landlocked derivatives of *G. maculatus*.

Although the three species look very similar, there are marked differences in body proportions and meristic characters. The divergence which has taken place since *G. usitatus* and *G. gracilis* became landlocked indicates that the species are plastic in their general morphology. *G. gracilis*, for instance, appears to have traversed the full range of vertebral number seen in the New Zealand Galaxiidae. *G. maculatus* represents a maximum, with 59–64, and *G. gracilis* a minimum for the family in New Zealand, with only 47–50. The argument that this is evidence that *G. gracilis* is not closely related to *G. maculatus* conflicts with the evidence of their obvious similarity; and in view of the known relationship between vertebral number and developmental temperatures, basing affinities on vertebral number must be regarded as suspect. *G. gracilis* has diverged further from *G. maculatus* than has *G. usitatus*. This is in accord with the apparent ages of the small lakes in which these species are found. Lake Rototuna (*G. gracilis*) occurs in well-stabilized, rolling sand dunes, once covered with bush, and at an altitude of about 90 m. It is probably older than Lake Waiparera (*G. usitatus*), which occurs in still shifting sand dunes, no more than 36 m above sea level.

Some workers, e.g., Whitley and Phillipps (1940: 229) and Phillipps (1940: 39), have suggested that *G. castlae* Whitley and Phillipps (=*G. brevipinnis* Günther) and *G. paucispondylus* are also landlocked derivatives of *G. maculatus*. Present understanding of the nature of the fauna suggests that this is most unlikely, and I think that *G. maculatus* and its two derivatives belong in a quite distinct species group.

A second species group includes three very similar large, stout-bodied species,

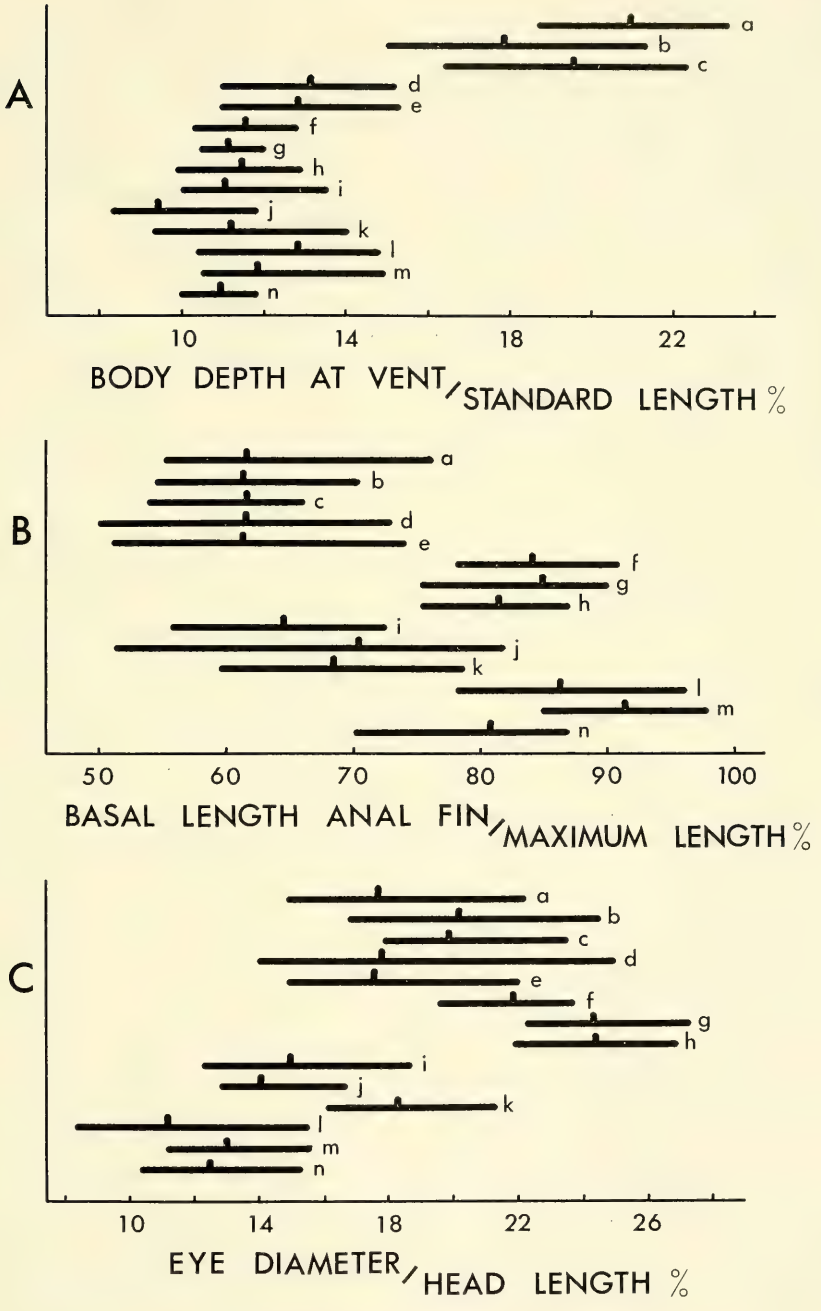


Figure 45. Species groups in the New Zealand Galaxiidae, as indicated by body proportions. a, *Galaxias argenteus*; b, *G. fasciatus*; c, *G. postvectis*; d, *G. brevipinnis*; e, *G. vulgaris*; f, *G. maculatus*; g, *G. gracilis*; h, *G. usitatus*; i, *G. paucispondylus*; j, *G. prognathus*; k, *G. divergens*; l, *Neochanna apoda*; m, *N. diversus*; n, *N. burrowsius*.

which are mostly lowland dwelling. These species, *G. argenteus,* (Fig. 4), *G. fasciatus* (Fig. 6), and *G. postvectis* (Fig. 9), form a compact group with their long, truncated to emarginate caudal fins, expansive dorsal and anal fins, and very long pectoral and pelvic fins, deep bodies (Fig. 45A, a, b, c), short and very deep caudal peduncles, and rather long, broad heads. The accessory lateral line is developed, and in all three, a large, dark, blue-black blotch above and behind the pectoral fin base is present. They all spawn in the autumn, are diadromous, and are found in rather similar habitats. The three species have almost identical ranges, and their characters strongly suggest common ancestry. But explaining their divergence within the New Zealand region is a problem for which I see no solution. It is difficult to imagine how allopatry could have developed, since all three species occur together in a common marine pool, migrate into fresh water in mixed species shoals, and are found together in the adult habitats. It is no simpler to see how speciation could have occurred had all three species remained sympatric. Even if a satisfactory model for sympatric speciation were to be constructed, this would necessarily involve habitat, reproductive, or behavioral differences of a nature and degree that seem to be lacking in these species. The only alternative is that these fishes invaded New Zealand from Australia several times, giving rise to the three stout-bodied species. Their great predominance on the west coast of New Zealand (see Fig. 7) suggests that they have evolved in the swift, rocky bush streams there, rather than in the very different plains streams of the southeast, where they are largely absent.

In the Australian galaxiid fauna, *G. truttaceus* Valenciennes shares many of the morphological characteristics of the stout species and is a suitable ancestral type; as it has a marine whitebait juvenile (Lynch, 1965), it also has the necessary dispersal ability. Since the larval stages of the three New Zealand stout-bodied species are believed to spend many months in the sea, giving them plenty of time to disperse from Australia, and since the East Australian-Tasman currents may be favorable for such dispersal, multiple dispersal of fishes ancestral to the stout species is quite comprehensible. Castle (1963: 13) suggested that the New Zealand freshwater eels (*Anguilla* spp.) probably spawn somewhere in the tropical Pacific, northeast of the New Hebrides; it would thus be the action of these currents which bring the leptocephali to New Zealand coasts—and they come in colossal numbers. The efficacy of these currents in dispersing fishes to New Zealand from the northeast seems demonstrated.

Skrzynski (1967) and others have reported the following New Zealand species from the Chatham Islands, 420 miles east of New Zealand: *G. fasciatus, G. argenteus, G. brevipinnis,* and *G. maculatus,* as well as *Gobiomorphus huttoni* (Ogilby), *Retropinna retropinna* (Richardson), *Anguilla australis schmidtii* Phillipps, *A. dieffenbachii* Gray, and *Geotria australis* Gray. Thus, unless these fishes have been on the islands since they were connected to mainland New Zealand, there must have been a great deal of dispersal to the islands from New Zealand, demonstrating considerable dispersal powers.

If *Galaxias argenteus, G. fasciatus,* and *G. postvectis* have each reached New Zealand from Australia, with a common ancestry there, these dispersals must have been at sufficiently separated intervals to permit reproductive isolation to develop between successive invasions. In comparison with the ideas of earlier workers on galaxiid fishes, that they must have reached New Zealand by means of land bridges, Gondwanaland, continental drift, etc., the idea of dispersal on several occasions is radical. But it is clear that there was a separate dispersal to bring *G. maculatus;* perhaps it is necessary to envisage independent dispersals for each of the three

stout-bodied species. If so, then the minor habitat and morphological differences between the three species are likely to be a product of interspecific competition forcing the three rather similar, sympatric species to specialize in some way. There is something inherently dissatisfying about the hypothesis of multiple invasions without any radiation of the group in New Zealand, but the formulation of a model allowing their speciation in New Zealand, either sympatrically or involving the development of geographic or other barriers to gene flow, eludes me.

Looking at the entire New Zealand fish fauna, it appears that it is almost entirely an invasion of fauna, with little speciation in the New Zealand region. Moreland (1958) has shown that only 30 per cent of the fauna is endemic. Since 7 per cent of the fauna is freshwater, and about 94 per cent of the freshwater fishes are endemic, it follows that only about 24 per cent of the marine fauna is endemic. Analysis of the fauna from Phillipps (1927a) shows that about 100 families, 200 genera, and 318 species occur in the fauna; thus there are two genera per family, and one and one half species per genus. Nearly one half of the genera have only one New Zealand species. Both the low endemism and the structure of the fauna suggest that the fauna is derived more by invasion from outside than from evolution within the New Zealand region (there is only one doubtful endemic marine fish family), and it is necessary to postulate fishes crossing the Tasman Sea a great number of times. Since, according to Moreland (1958: 28) 31 per cent of the species are presently shared with southeast Australia, recent trans-Tasman crossings must number in the vicinity of 100. The Galaxiidae, with their long-lasting oceanic, pelagic stages are admirably fitted for this dispersal, which may have occurred several times.

G. brevipinnis has many characteristics also found in the stout-bodied species, but it is much more slender (Fig. 45A, d). In addition to being widespread in New Zealand, it is present on the Chatham Islands, 420 miles east of New Zealand, the Auckland Islands, 290 miles south of New Zealand, and Campbell Island, 150 miles southeast of the Auckland Islands. It has a marine whitebait and thus has potentiality for transoceanic dispersal, and its range in the New Zealand region shows that it is probably a more effective disperser than any other species of *Galaxias*, except *G. maculatus*. As indicated in discussing the taxonomy of *G. brevipinnis*, I think that *G. weedoni* should become a synonym; if these two species are not conspecific, they are certainly very closely related, and *G. brevipinnis* is derived from *G. weedoni*.

Assuming that *G. brevipinnis* originated in the Australian region, it is necessary to explain its present distribution. As with the other species, it must have arrived in the New Zealand region in the East Australian and Tasman currents. Dispersal of fishes from New Zealand to the Chatham Islands does not appear too difficult, judging from the number of fishes that have succeeded in doing so. The difficult dispersal seems to be that to the sub-Antarctic islands—Campbell Island and the Auckland Islands. Dispersal from New Zealand is opposed by the west wind drift, which flows from west to east, south of New Zealand, with a substantial northern displacement, i.e., the Ekman drift (Burling, 1961, see his chart 1), which flows northeast from the sub-Antarctic islands, towards the south and east of New Zealand. It is possible that *G. brevipinnis* represents a direct dispersal from Australia to the islands; such a dispersal could have occurred if fishes in the East Australian current were picked up by the deeper west-east flowing west wind drift. The existence of a somewhat more extensive land area to the south of New Zealand, perhaps until late in the Tertiary, makes dispersal directly to the southern islands more plausible.

If *G. brevipinnis* was present in the sub-Antarctic islands prior to the Pleistocene

glaciations, its survival there during the glaciations becomes a critical question. If it became exterminated by the glacial ice cap, judging by existing current patterns, re-invasion of the islands from New Zealand would have been difficult, if possible. Gressitt (1964b: 11) reported that Campbell Island (the more southern of the two island groups) was "mildly glaciated during the Pleistocene . . . . there are cirques as well as glacial valleys but no proof of a continuous ice sheet." Gressitt (1964a: 548) thought that the fauna represented a depauperated fragment of an ancient subcontinental fauna, with over-sea colonization. Illies (1964: 215) examined the Plecoptera of Campbell Island, finding that "the existence of running freshwater environments on the island must have lasted at least since the break-down of land connections," i.e., for the present discussion, through the glaciations. This being the case, *G. brevipinnis* could probably have survived there too.

G. vulgaris is very similar in general form and appearance to *G. brevipinnis.* None of its body proportions are greatly different, although it is a little less depressed in the head region and the jaws are nearer equal in length. In the area where the two species are sympatric, it has fewer vertebrae, fewer rays in some fins, and shorter gill rakers, but these are all minor differences. The most significant difference is in the life history: *G. vulgaris* spawns in the spring and has no marine whitebait stage. This might seem a major difference, which precludes relationship between *G. vulgaris* and *G. brevipinnis;* yet Pollard (1966: 14) found that an apparently recent, landlocked derivative of *G. maculatus* in Victoria, Australia, has changed from autumn to spring spawning and from downstream to upstream migration prior to spawning. And this life history modification has been accompanied by very little morphological differentiation.

G. vulgaris is virtually restricted to the eastern side of the Southern Alps in the South Island, but it is very widespread in this area. This suggests that it must have evolved since the rise of the Southern Alps in the late Miocene and Pliocene. Its similarity to *G. brevipinnis* suggests that it is a derivative of this species, but how it diverged is unclear. *G. brevipinnis* and *G. vulgaris* are presently widely sympatric, since the former occurs in many lakes above the rivers in which the latter is found. The lacustrine populations of *G. brevipinnis* almost certainly post-date the Pleistocene glaciation. Apart from these lake populations, *G. brevipinnis* is very rare in the east of the South Island, and is probably sufficiently rare for isolation of some population(s) in one or several of the river basins which lack lacustrine populations of *G. brevipinnis* in the upper reaches. Such a happening may have allowed divergence of populations leading to *G. vulgaris.* Isolation may have been possible in some Canterbury rivers that do not flow directly into the sea, but disappear into coastal gravel, but this seems unlikely to have been a long-term condition in any particular river, such as would allow speciation.

There is a compact group of three small, slender, alpine species. They are confined to fresh, flowing water and do not have an obvious juvenile-adult metamorphosis. They are widespread in the southern half of the North Island and the northwest of the South Island, and extend over the Southern Alps into alpine Canterbury. This group comprises *G. divergens, G. paucispondylus,* and *G. prognathus.* Body proportions like slender trunk, very long and slender caudal peduncle, anterior dorsal fin insertion, short head with broad, shallow gape, short anal fin, bring these species together. Meristics are generally low. Of particular interest is the number of pelvic rays. *G. divergens* consistently has six rays, and although the two other species usually have seven, a high proportion of *G. paucispondylus* examined had six rays. In both *G. prognathus* and *G. paucispondylus* it was found that when there were seven

rays present, the ray in each fin closest to the ventral midline was commonly much reduced and often unbranched. This is interpreted as illustrating the trend towards reduction in the number of pelvic fin rays, a process that has become absolute at six rays in *G. divergens*. In these species, the anteriormost of the interorbital pores on the head has migrated to a position very close to the posterior nostril. In *G. divergens*, and sometimes in the other two species, the opening of this pore has become confluent with that of the nostril. This is a trend not seen in any other New Zealand species; the pore and nostril are always well separated. A further significant character that unites these species is the loss of the postcleithrum in the pectoral girdle. Occasionally there is a barely staining splint, but usually the postcleithrum does not appear in alizarin-stained adult specimens. It is present, though, in all other New Zealand galaxiids. In addition, the supraethmoid has a characteristic irregular shape, the palatine lacks the process that in other galaxiids runs along the side of the face lateral to the mesopteryoid, the mesopterygoid and metapterygoid do not meet in the posterior corner of the orbit but are separated by a band of cartilage, and there are no processes on the basioccipital. The species in this group exhibit some sympatry, *G. divergens* and *G. paucispondylus* being completely allopatric, but *G. prognathus* more or less bridging the geographic break between the other two.

There is little question that these species have a common ancestry, probably in a species similar to *G. paucispondylus* or *G. divergens*, which are more generalized than *G. prognathus*. Our present knowledge of their ranges may not be sufficiently complete to allow valid conclusions about their evolution. In particular, the two disjunct localities known for *G. prognathus* strongly suggest that further localities remain to be discovered in the intervening area, especially since the rivers there are superficially similar to those in which *G. prognathus* has already been found.

The present range of this species group suggests that the ancestral form had spread over the Wellington-Nelson-Buller region during or since the uplift of the Southern Alps. Their preference for cold alpine streams indicates that they may have evolved during the cold Pliocene-Pleistocene periods, and Fleming (1962: 81) considered that the "climax of the Kaikoura orogeny" occurred during the Pliocene. The existence of a single population (of *G. divergens*) in the east of the Volcanic Plateau far north of other known populations is a problem. Fleming showed that the marine transgression of the Miocene persisted into the Pliocene, covering the southern half of the North Island, from Taranaki to northern Hawke's Bay, except for the Wellington area, which was emergent and connected with the Nelson-Buller district. The northern population is conspecific with *G. divergens*, in which the pelvic fin ray number is only six, suggesting that this species must have spread north as the southern half of the North Island emerged towards and during the Pleistocene. It seems unlikely that this disjunction is a result of any earlier geological event, like the Miocene transgression; it is probably due either to destruction of the populations in the intermediate area—inland Hawke's Bay and northern Wairarapa—by the known, recent volcanic activity, or to incomplete knowledge of the range of the species.

G. divergens occurs in the south of the Bay of Plenty, the Wellington Province on both sides of the mountain ranges, and the northwest of the South Island as far south as the Buller River System at Maruia. *G. prognathus* is presently known only from the Buller River System at Maruia and the Rakaia System over on the eastern side of the Southern Alps. *G. paucispondylus* occurs in several river systems along the eastern side of the Alps.

This distribution pattern gives the im-

pression of a single, widespread species whose range became fragmented by the development of geographical barriers. If the ancestor of these species was widespread in the Nelson-Buller-northeast Canterbury regions during the rise of the Southern Alps, it would have been divided into two isolated series of populations by the mountains. Such a division would have sufficed to allow the divergence that has taken place between *G. paucispondylus* and *G. divergens.*

G. prognathus, in its remarkably elongated lower jaw, is, in some ways, the most specialized species of *Galaxias* in the New Zealand fauna. Its specialization suggests that it may have been in competition with another, similar species, like *G. paucispondylus* or *G. divergens.* It is almost certainly derived from one of them and the most recent species of the three.

G. vulgaris is distributed east of the ranges in the South Island, but it has invaded the west, in the upper Buller River System, in the Maruia River. This seems likely to have occurred since the rise of the Alps, for two reasons. First, the Maruia population shows very little divergence from those on the east, certainly less than that seen between various populations in the east; in other words, its derivation from the east seems to be very recent. In addition, the fact that *G. vulgaris* is present only in one western river system, and the fact that this river drains the lowest existing pass in the northern alps, suggests that *G. vulgaris* has crossed the alps from east to west, and recently.

The derivation of *G. prognathus* from either *G. divergens* or *G. paucispondylus* seems most simply accounted for if we presume that the parental species of *G. prognathus* was able to cross the alps. This would have brought *G. divergens* and *G. paucispondylus* into sympatry. If they had only recently become reproductively isolated, competition is likely to have been intense, forcing one of the species, probably the invader, to specialize, leading to *G. prognathus.* Since *G. prognathus* is now recorded from both sides of the Alps, it must also have recrossed the divide, and if it did evolve in competition with either *G. paucispondylus* or *G. divergens,* it is not very obvious on which side it is likely to have evolved. If it evolved on the east and has reinvaded the west, there is nice agreement with the distribution pattern of *G. vulgaris,* since both species are known in the west only from the Maruia River, in the upper reaches of the Buller River System, near the Lewis Pass. It appears too much of a coincidence that both these species are known in the west only from this one river, and that the river's headwaters drain the most easily crossed pass in the Alps. Stream capture seems quite feasible in the Lewis Pass area, and I am advised (P. M. Johns, pers. comm.) that there is a swampy area in the pass between the headwaters of the rivers on each side. I think that both *G. vulgaris* and *G. prognathus* have quite recently crossed from east to west and that *G. prognathus* probably evolved in the east. If so, I suspect that *G. prognathus* will be found in further alpine Canterbury rivers, particularly the upper tributaries of the Waiau, Hurunui, and Waimakariri Rivers.

An alternative hypothesis, which is feasible but without obvious support from physiographic changes, is that the two species in the east evolved in separate river basins and have subsequently become sympatric, as the rivers wandered back and forth across the Canterbury Plains and various pairs of rivers became confluent for a time. These river changes must be the mechanism behind the present broad range of *G. vulgaris,* but, inasmuch as they have not sufficed to produce speciation in *G. vulgaris,* it seems unlikely that isolation of any basin has been of sufficient duration to allow the contained populations to evolve reproductive isolation.

The final species group comprises the three species of *Neochanna—N. burrow-*

sius, N. apoda and *N. diversus*—which present a distinctive facies. They have an elongate and rounded trunk, somewhat blunt and little depressed head, small eye (Fig. 45C, 1, m, n), and a prominent development of the tubular anterior nostril, which may extend forwards beyond the upper lip. The dorsal and anal fins (Fig. 45B, 1, m, n) are rather long and low, with extremely thick, fleshy bases, the caudal fin is much rounded, and the peduncle flanges are very strongly developed, more or less confluent with the dorsal and anal fins. In *N. apoda* and *N. diversus* the pelvic fins and girdle have disappeared, and there are usually no mesopterygoidal teeth. The process of reduction is less complete in *N. burrowsius*, which has very small pelvic fins with only four or five rays, and only a few, small mesopterygoidal teeth, or none at all. Stokell (1945: 132) discussed the question of whether these three species form a natural phylogenetic unit, or whether their similarities are a case of convergence. He concluded that "if *burrowsius* is to be regarded as indicating the line of descent of *Neochanna* from *Galaxias*, it might be expected that a dominantly four rayed form, or a form lacking ventral fins but retaining vestiges of the pelvic bones would exist to indicate a further stage in the process of degeneration." As Stokell found, there is no such intermediate stage, and this is what students of evolution have commonly, if not normally, found. In this instance, it seems to indicate that a widespread species, ancestral to all three, had reached a stage of modification about equivalent to that exhibited by *N. burrowsius*. After the populations making up *N. burrowsius* were isolated, the modification continued, producing the other species of *Neochanna*, again probably from a common stock. A cursory examination of the three species shows that they are very similar to each other, certainly far more similar to each other than any one is to any New Zealand species of *Galaxias*.

It seems likely that the common ancestor of the neochannoid species was widespread in New Zealand in the Miocene as the marine transgression began. From this time onwards, the transgressions and great orogenies that followed would have fragmented its range. The populations now known as *N. burrowsius* would have been isolated from populations in the north and west by the rise of the main South Island mountain ranges in the late Miocene and Pliocene, and were perhaps restricted to the present small pocket in the Canterbury Province by the cold of the glaciations. Following this, the populations in the north and west lost the already reduced mesopterygoidal teeth and pelvic fins. During the Pliocene, the marine transgression covered most of the southern half of the North Island, and the transgression would have isolated populations—in the north of the North Island, leading to *N. diversus*, and in the Nelson-Buller-West Coast area, leading to *N. apoda*. Land connections between the North and South Islands lasting into the Pleistocene would have allowed *N. apoda* to reach the southern North Island, if it was not already present.

The preceding discussion suggests some probable species groups and their phylogenetic relationships, and thereby establishes possible terminal branching points in the phylogeny of the species (Fig. 46). It seems almost certain that three of these branching systems, those containing (1) *G. maculatus* and its derivatives, (2) the stout-bodied species, and (3) *G. brevipinnis* and *G. vulgaris*, originated independently in Australia; *G. maculatus* occurs in Australia, the stout-bodied species seem to be derived from *G. truttaceus*, and *G. brevipinnis* is derived from *G. weedoni* or is conspecific with it.

There are two other very closely knit and distinctive species groups in the New Zealand fauna. There is no evidence to suggest where the slender, alpine species originated. The neochannoid species have counterparts in the Tasmanian fauna, presently treated by Scott (1936: 160) as two

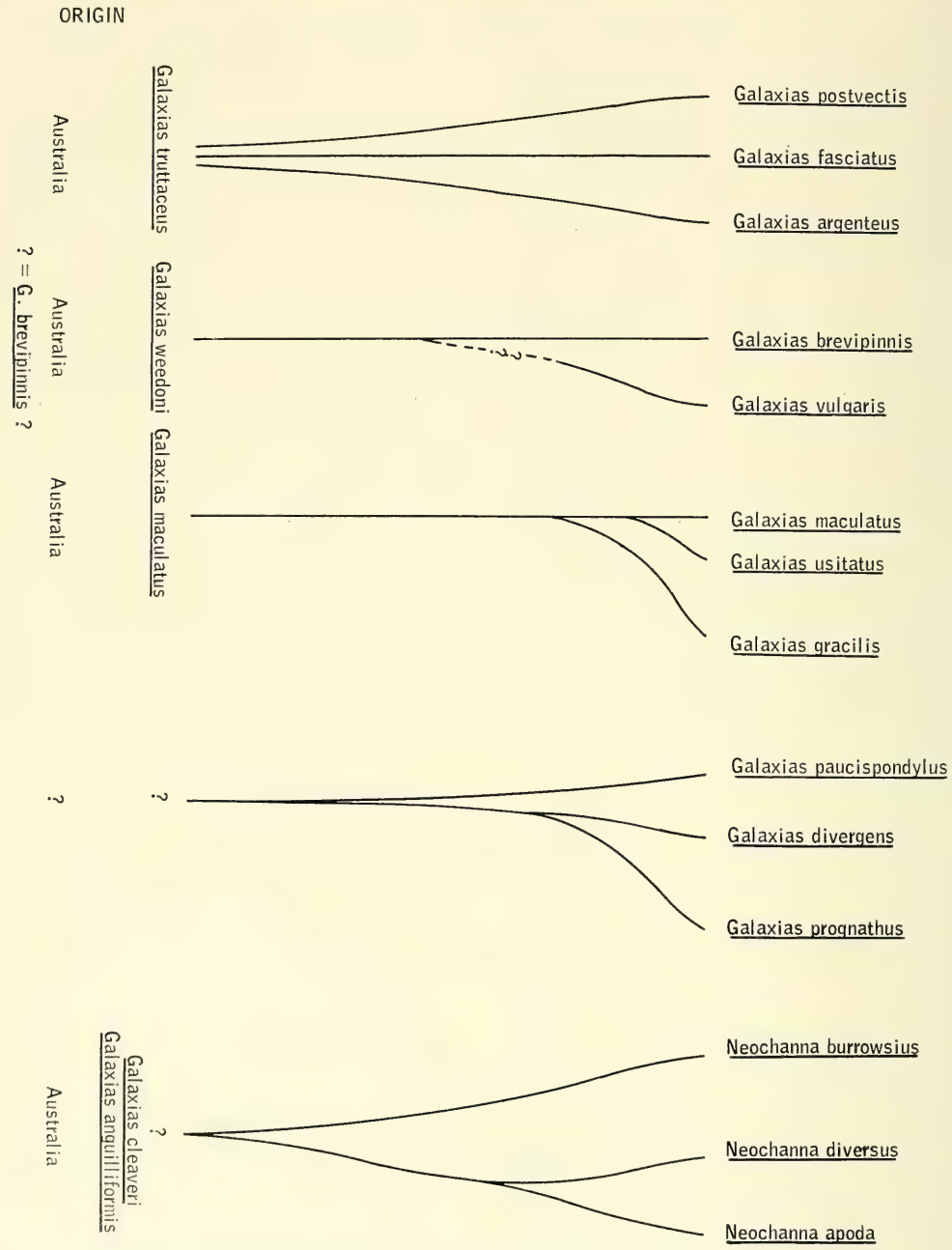


Figure 46. Suggested phylogenetic relationships of the New Zealand species of *Galaxias* and *Neochanna*.

species of *Saxilaga*. If, as workers like Fleming (1963: 382) claim, the ratite birds, *Sphenodon*, *Leiopelma*, and other animals dispersed to New Zealand across the sea, then it is possible that a neochannoid species, even though it does not possess a definite sea-going stage, could have rafted or otherwise dispersed to New Zealand.

Presently, nothing is known about the euryhalinity of either New Zealand or Tasmanian species of this group, but it is certain to be much greater than that of *Leiopelma*, a small frog. If the Australian species, treated by Scott (1936) as the distinct genus *Saxilaga* (also said to include *N. burrowsius* from New Zealand and *G. globiceps* Eigenmann from Chile), have a common origin with *Neochanna* in New Zealand, it may be necessary to alter the generic arrangement of these species. The answer does not, however, seem to lie in whether *G. cleaveri* Scott and *G. anguilliformis* Scott belong in the genus *Saxilaga*, but in whether or not it is preferable to regard them as species of *Galaxias*, showing evolutionary trends towards *Neochanna*, or to include them in *Neochanna*, as a distinct radiation of "mudfishes." If these species do form a natural grouping, it seems natural to include them all in *Neochanna*. The inclusion of *G. globiceps* in this assemblage is supported neither by Eigenmann's description nor by his figure of the species. Before these problems can be clarified, the osteology of these species needs study.

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LITERATURE CITED

Barnard, K. H. 1943. Revision of the indigenous fishes of the south-west Cape Region. Ann. South African Mus. **36**(2): 101–263.

Benzie, V. 1961. A comparison of the life history and variation in two species of *Galaxias, G. attenuatus* and *G. vulgaris*. Unpublished thesis, University of Canterbury, Christchurch, New Zealand. 193 pp.

Berg, L. S. 1940. The classification of fishes, both recent and fossil. Trav. Inst. Zool. Acad. Sci. U.S.S.R. **5**(2): 1–517. (Reprint Edwards, Ann Arbor, 1947.)

Bigelow, H. B., and W. C. Schroeder. 1963. Family Osmeridae. *In*: Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. **1**(3): 553–597.

Bloch, M. E., and J. G. Schneider. 1801. Systema Ichthyologicae Iconibus cx Illustratum. Schneider, Berlin, 584 pp., 110 pls.

Breder, C. M., and D. E. Rosen. 1966. Modes of Reproduction in Fishes. Natural History Press, New York, 941 pp.

Boulenger, G. A. 1902. The explanation of a remarkable case of geographical distribution in fishes. Nature **67**(1726): 84.

Burling, R. W. 1961. Hydrology of circumpolar waters south of New Zealand. New Zealand Dept. Sci. Ind. Res. Bull. **143**: 1–66.

Burnet, A. M. R. 1965. Observations on the spawning migration of *Galaxias attenuatus* (Jenyns). New Zealand J. Sci. **8**(1): 79–87.

Cairns, D. 1942. Life history of the two species of fresh water eel in New Zealand. II. Food and interrelationships with trout. New Zealand J. Sci. Tech. **23**: 132–148.

Castle, P. H. J. 1963. Anguillid leptocephali in the southwest Pacific. Zool. Pubs. Vict. Univ. Wellington (N. Z.) **33**: 1–14.

Chapman, W. M. 1944. The osteology and relationships of the South American fish *Aplochiton zebra* Jenyns. J. Morph. **75**(1): 149–165.

Clarke, F. E. 1899. Notes on Galaxidae, more especially those of the western slopes, with descriptions of new species. Trans. Proc. New Zealand Inst. **31**: 78–91.

Cunningham, B. T. 1951. Preliminary report on fishes. *In*: The New Zealand-American Fiordland expedition (A. L. Poole, ed.). New Zealand Dept. Sci. Ind. Res. Bull. **103**: 1–99.

Cuvier, G. 1817. Les Galaxies. *In*: Le regne animal, Vol. 2, pp. 282–283. Deterville, Paris, 4 vols.

Cuvier, G., and M. A. Valenciennes. 1846. Hist. Nat. Poissons Vol. 18, pp. 508–511. Levrault, Paris, 22 vols, 8°.

Davidson, M. M. n.d. Anatomy of *Neochanna apoda* Günther, Galaxiidae. Typewritten MS, Library of Fisheries Research Division, New Zealand Marine Department, Wellington, New Zealand.

Dieffenbach, E. 1843. List of fishes hitherto detected on the coasts of New Zealand by John Richardson with descriptions by J. E. Gray and Dr. Richardson of the new species brought home by Dr. Dieffenbach. *In*: Travels in New Zealand. Murray, London, 2 vols.

Dollimore, E. S. 1962. The New Zealand Guide. Wise, Dunedin, 981 pp.

Eldon, G. A. 1968. Notes on the presence of the brown mudfish (*Neochanna apoda* Günther) on the west coast of the South Island of New Zealand. New Zealand J. Mar. Freshw. Res. **2**: 37–48.

Fell, H. B. 1962. West wind drift dispersal of echinoderms in the Southern Hemisphere. Nature **193**(4817): 759–761.

———. 1967. Cretaceous and Tertiary surface currents of the oceans. Oceanogr. Mar. Biol. Ann. Rev. **5**: 317–341.

Fleming, C. A. 1962. New Zealand biogeography; a palaeontologist's approach. Tuatara **10**(2): 53–108.

———. 1963. Paleontology and southern biogeography. *In*: Pacific Basin Biogeography, pp. 369–385 (J. L. Gressitt, ed.). Bishop Museum, Honolulu.

Forster, J. R. 1778. Observations Made During a Voyage Round the World on Physical Geography, Natural History and Ethnic Philosophy. Robinson, London, 649 pp.

———. 1844. Descriptiones Animalium. Lichenstein, Berlin, 424 pp.

Gmelin, J. F. 1789. Systema Naturae. Gmelin, Lipsiae, 3 vols., 13th ed.

Gosline, W. A. 1960. Contributions towards a classification of modern isospondylous fishes. Bull. British Mus. (Nat. Hist.) Zool. **6**(6): 327–365.

Gray, J. E. 1842. Three hitherto unrecorded species of fresh water fish brought home from New Zealand and presented to the British Museum by Dr. Dieffenbach. Zool. Misc., p. 73.

Greenwood, P. H., D. E. Rosen., S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. American Mus. Nat. Hist. **131**(4): 339–456, 3 pls.

Gressit, J. L. (ed.). 1963. Pacific Basin Biogeography. Bishop Museum, Honolulu, 561 pp.

———. 1964a. Insects of Campbell Island. Pac. Insects Monogr. **7**: 1–663.

———. 1964b. Introduction. *In*: Insects of Campbell Island, pp. 1–33. Pac. Insects Monogr. **7**: 1–663.

Günther, A. 1866. Catalogue of the Fishes in the Collection of the British Museum, Vol. 6. British Museum, London, 8 vols.

———. 1867. On a new form of mudfish from New Zealand. Ann. Mag. Nat. Hist. (3)**20**: 305–309, 1 pl.

Haast, J. von. 1872. Notes on some undescribed fishes from New Zealand. Trans. Proc. New Zealand Inst. **5**: 272–278.

Hector, J. 1869. Comment on *Neochanna apoda*. Trans. Proc. New Zealand Inst. **2**: 402.

———. 1902. Notes on New Zealand whitebait. Trans. Proc. New Zealand Inst. **35**: 312–319.

Hefford, A. E. 1931a. Whitebait. Rep. Fish. New Zealand **1930**: 15–16, 21–23.

———. 1931b. Whitebait. Rep. Fish. New Zealand **1931**: 14–17.

———. 1932. Whitebait investigation. Rep. Fish. New Zealand **1932**: 14–15.

Henderson, N. E. 1967. The urinary and genital systems of trout. J. Fish. Res. Bd. Canada **24**(2): 447–449.

Hoar, W. S. 1957. Gonads and reproduction. *In*: The Physiology of Fishes (M. E. Brown, ed.). Academic Press, New York, 2 vols.

Hollister, G. 1934. Clearing and staining fish for bone study. Zoologica **12**(10): 89–101.

Hope, D. 1928. Whitebait (*Galaxias attenuatus*); growth and value as trout food. Trans. Proc. New Zealand Inst. **58**: 389–391, 2 pls.

Hopkins, C. L. 1965. Feeding relationships in a mixed population of fresh water fish. New Zealand J. Sci. **8**: 149–157.

Hubbs, C. L. 1953. Antitropical distribution of fishes and other organisms. Proc. Seventh Pacific Sci. Congr. **3**: 324–329.

Hubbs, C. L., and K. F. Lagler. 1947. Fishes of the Great Lakes Region. Cranbrook Inst. Sci. Bull. **26**: 1–186, pls.

Hutton, F. W. 1872. Catalogue with diagnoses of species. *In*: Fishes of New Zealand (J. Hector and F. W. Hutton). Colonial Museum and Geological Survey, Wellington, 133 pp., 12 pls.

———. 1874. Notes on some New Zealand fishes. Trans. Proc. New Zealand Inst. **6**: 104–107.

———. 1889. List of New Zealand fishes. Trans. Proc. New Zealand Inst. **22**: 275–285.

———. 1896. Notes on some New Zealand fishes with description of a new species and a synopsis of the New Zealand species of *Galaxias*. Trans. Proc. New Zealand Inst. **28**: 314–318.

———. 1901. On a marine *Galaxias* from the Auckland Islands. Trans. Proc. New Zealand Inst. **34**: 198–199.

———. 1904. Index Faunae Novae Zealandiae. Dulau, London, 372 pp.

Illies, J. 1964. Insecta—Plecoptera. *In*: Insects of Campbell Island, pp. 208–215. (J. L. Gressitt, ed.). Pac. Insects Monogr. **7**: 1–663.

Jordan, D. S. 1919. The genera of fishes, part II, from Agassiz to Bleeker, 1833–1858, twenty six years with the accepted type of each. A contribution to the stability of scientific nomenclature. Leland Stanford Junior University Publication, University Series. pp. 163–284.

Jenyns, L. 1842. The Zoology of H. M. S. *Beagle* During 1832–6. Part 4. Fish. Smith, Elder, London, 151 pp.

Kendall, W. C. 1922. Peritoneal membranes, ovaries and oviducts of salmonoid fishes and their significance in fish culture practices. Bull. United States Bur. Fish. **37**: 185–208.

———. 1935. The fishes of New England. The Salmon family II. The salmons. Mem. Boston Soc. Nat. Hist. **9**(1): 1–166, 11 pls.

Kner, R. 1865. Reise der Österreichischen Fregatte *Novara* um die Erde in den Jahren 1857–59. Zoologischer Theil, Fische. Wien, 433 pp., 16 pls.

Lagler, K. F., J. E. Bardach, and R. R. Miller. 1962. Ichthyology, the Study of Fishes. Wiley, New York, 545 pp.

Lindsey, C. C. 1961. The bearing of experimental meristic studies on racial analyses of fish populations. Proc. Ninth Pacific Sci. Congr. **10**: 54–58.

Lynch, D. D. 1965. Changes in Tasmanian fishery. Australian Fish. Newslett. **24**(4): 13, 15.

McDowall, R. M. 1964a. The affinities and derivation of the New Zealand fresh water fish fauna. Tuatara **12**(2): 56–67.

———. 1964b. A consideration of the question "What are whitebait?" Tuatara **12**(3): 134–156.

———. 1965a. The composition of the New Zealand whitebait catch, 1964. New Zealand J. Sci. **8**(3): 285–306.

———. 1965b. Studies on the biology of the red finned bully, *Gobiomorphus huttoni* (Ogilby), III, Food studies. Trans. Roy. Soc. New Zealand Zool. **5**(17): 233–254.

———. 1966a. Further notes on *Galaxias* whitebait and their relation to the distribution of the Galaxiidae. Tuatara **14**(1): 12–18.

———. 1966b. A guide to the identification of New Zealand fresh water fishes. Tuatara **14** (2): 89–104.

———. 1967a. New land-locked fish species of the genus *Galaxias* from North Auckland, New Zealand. Breviora **265**: 1–11.

———. 1967b. Some points of confusion in galaxiid nomenclature. Copeia **1967**(4): 841–843.

———. 1968a. Interactions of the native and alien faunas of New Zealand and the problem of fish introductions. Trans. American Fish. Soc. **97**: 1–11.

———. 1968b. *Galaxias maculatus* (Jenyns); the New Zealand whitebait. New Zealand Mar. Dep. Fish. Bull. (new series) **2**: 1–84.

———. 1969. Relationships of galaxioid fishes, with a further discussion of salmoniform classification. Copeia **1969**(4): 796–824.

McKenzie, D. H. 1904. Whitebait at the Antipodes. New Zealand Illustrated Mag. **10**: 122–126.

McKenzie, M. K. n.d. Embryonic and larval structures of *Galaxias attenuatus* (Jenyns). Unpublished thesis, Victoria University, Wellington, New Zealand, 74 pp., 24 pls.

McMillan, H. M. 1951. The osteology and relationships of the family Retropinnidae Gill. Unpublished thesis Canterbury University, Christchurch, New Zealand, 59 pp.

Moreland, J. M. 1958. Composition, distribution and origin of the New Zealand fish fauna. Proc. New Zealand Ecol. Soc. **6**: 28–30.

Myers, G. S. 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia **1949**(2): 89–97.

Muller, J. 1844. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. Abhandl. Akad. Wiss. Berlin **1844**: 117–216.

Ogilby, J. D. 1899. Contributions to Australian ichthyology. Proc. Linn. Soc. New South Wales **24**(1): 154–186.

Okada, Y. 1960. Studies on the Freshwater Fishes of Japan. Mie Prefectural University, Mie, 860 pp., 61 pls.

Oliver, W. R. B. 1936. The tertiary flora of the Kaikorai Valley, Otago. Trans. Roy. Soc. New Zealand **66**(3): 284–304.

Phillipps, W. J. 1919. Life history of the fish *Galaxias attenuatus*. Australian Zool. **1**(7): 211–213.

———. 1923. Note on the occurrence of the New Zealand mudfish or hauhau, *Neochanna apoda*. New Zealand J. Sci. Tech. **6**(1): 62–63.

———. 1924a. The New Zealand minnow. New Zealand J. Sci. Tech. **7**(2): 117–119.

———. 1924b. The koaro, New Zealand's subterranean fish. New Zealand J. Sci. Tech. **7** (3): 190–191.

———. 1926a. Second occurrence of *Galaxias robinsonii* in New Zealand. New Zealand J. Sci. Tech. **8**(2): 98–99.

———. 1926b. Additional notes on fresh water fishes. New Zealand J. Sci. Tech **8**(4): 289–298.

———. 1926c. New or rare fishes of New Zealand. Trans. Proc. New Zealand Inst. **56:** 529–537, 6 pls.

———. 1927a. Bibliography of New Zealand fishes. New Zealand Mar. Dep. Fish. Bull. **1:** 1–68.

———. 1927b. A checklist of the fishes of New Zealand. J. Pan-Pacific Res. Inst. **2**(1): 9–16.

———. 1940. The Fishes of New Zealand, vol. 1. Avery, New Plymouth, 87 pp.

Pollard, D. A. 1966. Land-locking in diadromous salmonoid fishes with special reference to the common jollytail (*Galaxias attenuatus*). Australian Soc. Limn. Newslett. **5**(1): 13–16.

Powell, L. 1869. On four fishes commonly found in the River Avon, with a consideration of the question "What is whitebait?" Trans. Proc. New Zealand Inst. **2:** 84–87.

Regan, C. T. 1905. A revision of the fishes of the family Galaxiidae. Proc. Zool. Soc. London **2:** 363–384, 4 pls.

———. 1909. The classification of teleostean fishes. Ann. Mag. Nat. Hist., ser. 8, **3:** 75–86.

———. 1911. The Fresh Water Fishes of the British Isles. Methuen, London, 287 pp., 37 pls.

Reid, R. C. 1886. Rambles on the Golden Coast of the South Island, New Zealand. Colonial Printing and Publishing, London, 176 pp.

Rendahl, H. 1926. Fishes from New Zealand and the Auckland and Campbell Islands. Papers Dr. Mortensen's Pacific Exped. 1915–1916 **30:** 1–14.

Richardson, J. 1843. Report on the present state of the ichthyology of New Zealand. Rep. British Assn. **12:** 12–30.

———. 1848. Ichthyology of the voyage of H. M. S. *Erebus* and *Terror*. *In*: The Zoology of the *Erebus* and *Terror* During the Years 1839–43. Longman, Brown, Green and Longman, London.

Riney, T., J. S. Watson, E. G. Turbott, and W. E. Howard. 1959. Lake Monk expedition; an ecological study in southern Fiordland. New Zealand Dep. Sci. Ind. Res. Bull. **135:** 1–75.

Romer, A. S. 1966. Vertebrate Paleontology, 3rd ed. University of Chicago, Chicago, 468 pp.

Sauvage, H. E. 1880. Notice sur quelques poissons de l'île Campbell et l'Indo-Chine. Bull. Soc. Philom. ser. 7, **4:** 228–233.

Schoennherr, C. J. 1838. Genera et Species Curculionidum, Vol. 4, No. 2, p. 1043. Roret, Paris, 8 vols.

Scott, E. O. G. 1934. Observations on some Tasmanian fishes with descriptions of new species. Pap. Roy. Soc. Tasmania **1933:** 31–53, 2 pls.

———. 1936. Observations on fishes of the family Galaxiidae I. Pap. Roy. Soc. Tasmania **1935:** 85–112.

———. 1966. The genera of Galaxiidae. Australian Zool. **13**(3): 244–258.

Skrzynski, W. 1967. Fresh water fishes of the Chatham Islands. New Zealand J. Mar. Freshw. Res. **1**(2): 89–98.

Stokell, G. 1938. A new species of the genus *Galaxias* with a note on the occurrence of *Galaxias burrowsii* Phillipps. Rec. Canterbury Mus. (N.Z.) **4**(4): 203–208, 1 pl.

———. 1940. A new species of *Galaxias*. Trans. Roy. Soc. New Zealand **69:** 422–424.

———. 1945. The systematic arrangement of the New Zealand Galaxiidae. I. Generic and sub-generic classification. Trans. Roy. Soc. New Zealand **75**(2): 124–137.

———. 1949. The systematic arrangement of the New Zealand Galaxiidae. II. Specific classification. Trans. Roy. Soc. New Zealand **77**(4): 472–496, 12 figs.

———. 1950. Fresh water fishes from the Auckland and Campbell Islands. Cape Exped. Ser. Bull. (N.Z.) **9:** 1–8.

———. 1954. Contributions to galaxiid taxonomy. Trans. Roy. Soc. New Zealand **82**(2): 411–418, 1 pl.

———. 1955. Fresh Water Fishes of New Zealand. Simpson and Williams, Christchurch, 145 pp., 42 pls.

———. 1959a. Structural characters of Te Anau salmon. Trans. Roy. Soc. New Zealand **87** (3–4): 255–263, 2 pls.

———. 1959b. Notes on galaxiids and eleotrids with descriptions of new species. Trans. Roy. Soc. New Zealand **87**(3–4): 265–269, 2 pls.

———. 1960. The validity of *Galaxias postvectis* Clarke, with notes on other species.

Rec. Dom. Mus. New Zealand **3**(3): 235–239.

———. 1966. A preliminary investigation of the systematics of some Tasmanian Galaxiidae. Pap. Roy. Soc. Tasmania **100**: 73–79.

Swinnerton, H. H. 1903. The osteology of *Cromeria nilotica* and *Galaxias attenuatus*. Zool. Jahrb. **18**: 58–70.

Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. United States Nat. Mus. **122**(3596): 1–7.

Vollams, S. E. 1872. On the mudfish (*Neochanna apoda*). Trans. Proc. New Zealand Inst. **5**: 456–457.

Waite, E. R. 1907. Basic list of New Zealand fishes. Rec. Canterbury Mus. (N.Z.) **1**(1): 1–39.

———. 1909. Vertebrata of the sub-antarctic islands of New Zealand. *In:* The Subantarctic Islands of New Zealand (C. Chilton, ed.). Philosophical Institute of Canterbury, Christchurch, 2 vols.

Weitzman, S. H. 1967. The origin of the stomiatoid fishes with comments on the classification of salmoniform fishes. Copeia **1967** (3): 507–540.

Whitley, G. P. 1935. Whitebait. Victorian Nat. Melb. **52**(3): 41–51, 1 pl.

———. 1956a. The story of *Galaxias*. Australian Mus. Mag. **12**(1): 30–34.

———. 1956b. Name list of New Zealand fishes. *In*: Treasury of New Zealand Fishes (D. H. Graham), 2nd ed. Reed, Wellington, 424 pp.

———. 1956c. New fishes from Australia and New Zealand. Proc. R. Zool. Soc. New South Wales 1954–55: 34–38.

Whitley, G. P., and W. J. Phillipps. 1940. Descriptive notes on some New Zealand fishes. Trans. Roy. Soc. New Zealand **69**(2): 228–236, 2 pls.

Woods, C. S. 1966. Species composition of whitebait (*Galaxias* spp.). Rec. Canterbury Mus. (N.Z.) **8**(2): 177–179.

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ADDENDA

1). Since this work was completed, an extensive re-analysis of the taxonomy of *G. maculatus* and its lake derivatives in 16 lakes in Australia, New Zealand, and South America, has been made. This analysis suggested that *G. usitatus* McDowall (p. 382) is best regarded as a local race of *G. maculatus*, although the validity of *G. gracilis* McDowall (p. 384) is confirmed (McDowall, In Prep.).

2). Study of adult specimens of *G. weedoni* Johnston supported tentative suggestions (p. 364) that this species is a junior synonym of *G. brevipinnis* Günther, which is thus shown to have trans-Tasman range (McDowall, In Press, Records of the Dominion Museum, New Zealand, vol. 7).

3). A recent checklist of the fishes of New Zealand by G. P. Whitley (Australian Zoologist, vol. 15, 1968, pp. 1–102) listed as valid several *Galaxias* species synonymized by myself and earlier authors, and is inaccurate and misleading.

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THE SPIDER GENUS *ARIADNA* IN THE AMERICAS (ARANEAE, DYSDERIDAE)

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INTRODUCTION

The spider family Dysderidae, to which the genus *Ariadna* belongs, is one of a series of presumably primitive families called the haplogyne spiders, from the simplicity of their genitalia. Other haplogyne families are the Plectreuridae, Diguetidae, Sicariidae, Scytodidae, Caponiidae and Oonopidae. (The families Leptonetidae, Ochyroceratidae, and Telemidae, often included in the haplogyne series, are possibly more closely allied to the Araneoidea, and are omitted from consideration here.)

Dysderids are medium- to large-sized spiders (maximum body length about 25 mm) of either sedentary or wandering habits. Their web is of the tubular retreat type, sometimes with radiating trip lines extending from the mouth, but containing no viscid silk, and not functioning as a snare. The spiders have six eyes (or no eyes, as in a few cave-dwelling species), two lungs, and a pair of tracheal spiracles close behind the lung apertures; they bear usually three, sometimes two, tarsal claws. The family is nearly cosmopolitan in distribution, but is absent or rare in polar and cold northern temperate regions.

The genus *Ariadna* is of interest because of its almost worldwide distribution, its occurrence on isolated islands, the many species that have been described, and the fact that it is haplogyne. The genitalic simplicity of haplogyne spiders makes identification of specimens, especially females, difficult. As a consequence, the taxonomy of the haplogyne families has been in a confused state until recently.

A revision of the American *Ariadna* was the principal objective of this study, in which, as far as possible, the males were distinguished by genitalia. A secondary objective, however, was a search for other taxonomic characters. Computer methods were used in this search and in the grouping of species, and the calculated results were compared with those obtained by a "classical" taxonomic approach (Beatty and Bossert, in prep.). Although the secondary objective is probably of more general interest and application, all phases of the study are, of course, closely interrelated.

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POSITION OF THE DYSDERIDAE AMONG THE HAPLOGYNE FAMILIES

The haplogyne spiders are readily separable into two groups that may deserve to be ranked as superfamilies. These groups are distinguished primarily by differences in chelicerae, posterior respiratory organs, and number of heart ostia.

In the Plectreuridae, Diguetidae, Sicariidae, and Scytodidae, the chelicerae are chelate and are joined to each other basally over one-fourth or more their length; a single median tracheal spiracle is situated behind the middle of the abdomen but not immediately adjacent to the spinnerets, and the heart has three pairs of ostia. Within this group, the Plectreuridae and Diguetidae are similar to each other in some characters, but differ strongly from the Sicariidae and Scytodidae. The latter families are close to each other morphologically.

In the Dysderidae, Oonopidae, and Caponiidae, the subchelate chelicerae are free from each other or are only barely connected by membrane proximal to the sclerotized part of the appendages; a pair of large tracheal spiracles is situated just behind the lung openings, and the heart has two pairs of ostia. Additional data are summarized in Table 25.

In the collection of the Museum of Comparative Zoology, I have examined a few unidentified specimens that do not appear to fit well into any of the recognized families. Many new species and some new genera almost certainly remain to be discovered, especially in south temperate regions. The intermediate structural characters of some of these species will probably discourage maintenance of seven separate families for the haplogyne spiders.

Within the haplogyne series, the Dysderidae are distinguishable from the sicariioid families by the characters listed above. They differ from the other two families as follows: from all the Caponiidae and a few of the Oonopidae by their having six eyes; from most of the six-eyed oonopids by the arrangement of the eyes; from both the Caponiidae and Oonopidae by their well-developed book lungs, the presence of a tarsal claw on the palp of the female, their larger size and sedentary habits, and their use of silk for making tubular retreat webs.

In habitus the larger dysderids seem primitive and similar to the plectreurids, filistatids, ctenizids, and liphistiids. Each of these other families is probably the most primitive living member of its particular suprafamilial group. The body size, leg proportions, color, sedentary retreat–web building habit, and genitalic simplicity of these five families, although far from providing conclusive evidence, certainly suggest relationship. I believe that a more intensive study of this group of families than has thus far been published would yield important data pertaining to the phylogeny of the Araneae.

NATURAL HISTORY OF *ARIADNA*

Members of the genus *Ariadna* are sedentary nocturnal spiders. Their tubular webs of closely woven pure white silk are slightly widened at the mouth, from which single threads radiate in all directions. These threads are attached to the substratum at distances of about two to ten millimeters from the tube. The spiders stand at the mouth of the tube at night or during periods of low light intensity during the day. They are highly sensitive to vibration of the radiating threads by potential prey, reacting with a rapid dash from the tube and back again. The movement is too swift to be followed precisely with the naked eye, but it appears that the spiders do not emerge completely from the tube. The prey is seized in the two anterior pairs of legs. The double rows of heavy spines on the ventral surfaces of the legs probably function in preventing the escape of the prey.

All species of *Ariadna* for which information is available place their webs in the same type of microhabitat: crevices and small holes. Depending upon the size of the spider, the diameter of the web ranges from one to about ten millimeters. The web is generally built in a crevice that has a width about equal to the diameter of the tube. On one occasion, however, I saw a web suspended vertically in the center of a pipe that had a diameter of about two inches. Levi (pers. comm.) reports that juvenile *A. maxima* in Chile often build their webs on top of each other, so that a series of tube webs spans a wide crevice. The spider is so abundant that this behavior may result from a shortage of crevices of a more appropriate size.

In my experience, broken outcrops of rock are the sites most favored by *Ariadna*, but not all kinds of rock are equally acceptable. Unstable rocks such as shale are avoided; massive thick-bedded rocks usually do not have enough crevices of sufficient depth to support more than a scattered individual or two. One of the largest colonies I have seen was on Gibraltar Island in western Lake Erie. At one end of the island a weathered, highly fractured dolomite cliff rises 15–20 feet (5–7 m) from the edge of the water. The accessible portion of this outcrop, about 50 feet (17 m) long, is occupied by hundreds of *A. bicolor* webs.

The amount of moisture present is also of considerable importance. I have never found *Ariadna* on a rock outcrop from which even a small amount of water was seeping, nor in highly insolated outcrops in the lowlands of the southwestern and Mexican deserts. At low elevations of 2700 to 4600 feet (820–1400 m) in southern Arizona, *A. pilifera* occurs sparingly in rocks along canyon bottoms. At higher elevations it gradually spreads to more

exposed outcrops. In the Santa Catalina Mountains north of Tucson, Arizona, I have taken it at a maximum elevation of 7500 feet (2280 m).

Ariadna is also commonly collected in crevices on buildings and other man-made structures. I have collected *A. bicolor* in such places in Ohio, North Carolina, Florida, and Illinois, and *A. pilifera* in Arizona. Crevices in or under tree bark and palm fronds are frequently used, although less often than the above microhabitats. *Ariadna fidicina* has been taken from beneath eucalyptus bark in California, and *A. arthuri* from under the bark of red mangrove in the Florida Keys.

Additional microhabitats include crevices and small holes found within and about clumps of moss, beneath rocks or boards on the ground, among roots and stems of grass clumps (Barnes, 1953), in ground litter, and once in shipworm burrows in a hatch-cover thrown up on a Florida beach. All of these sites are used much less frequently than the three mentioned above, and the population densities are relatively low.

Even where some member of the genus is abundant, suitable microhabitats are often so localized that the spider appears rare. In such cases it is usually found only in the more marginal kinds of microhabitats. A special search and special collecting methods are usually required to determine its actual frequency in a given area.

A rock outcrop fitting the description given earlier will usually harbor at least a few *Ariadna*, and populations as high as five to ten per linear foot of crevice are not unusual. When the webs have been located, one can usually catch a large number of specimens in a short time by using the technique described below.

The only equipment needed is an ordinary dissecting needle and a vial, or a series of vials with cotton plugs if the spiders are to be kept alive for a time. While holding the open mouth of a vial near, but not touching, the mouth of the web, thrust the needle quickly into the crevice at an oblique angle to the web, and as far back from the mouth of the web as possible. The object is to close off the web behind the spider, so that it can not escape from the rear of the web into the crevice. Place the mouth of the vial against the web opening, and gently work the needle forward. The spider will be driven forward and will usually make a quick dash from the web into the vial. If the collecting is done at night with the aid of a head-lamp, the spiders will be found sitting at the mouths of the web. Under these conditions they may be captured easily and quickly by the above method.

Two factors probably account for the colonial habit of *Ariadna*. The first is the relative scarcity and isolation of optimum microhabitats. The spiders are certainly present in many sub-optimum habitats, but in small numbers and thinly scattered. Second, no species of *Ariadna*, in fact no haplogyne spider of any kind, is known to balloon. The eggs of *Ariadna* are laid in the tube of the female and the young remain in the tube for some time after hatching. Judging from the size of known second-instar young and the smallest individuals found inhabiting their own tubes, I would guess that the juveniles leave the female's web between their second and third molts. Dispersal appears to vary from no more than a few millimeters to perhaps ten yards (10 m).

The food habits of *Ariadna* are virtually unknown. In captivity I have fed them leafhoppers, small moths, and *Drosophila*, all of which they took readily. The insects available in largest numbers to the Gibraltar Island colony are caddis-flies, midges, and Mayflies, which emerge from the lake in thousands during the summer. *Ariadna* is probably like many spiders in eating other spiders readily, also.

Courtship and mating in this genus have not been observed. Presumably it is similar to that of the related genera *Segestria* and *Dysdera*. Gerhardt (1921) described and

illustrated the mating behavior of *Segestria*. Males of this genus lack the spurs present on the anterior legs of some male *Ariadna*. The male pushes back the female's legs with his, moves under the female's carapace, and, holding the anterior part of her abdomen with his fangs, inserts both palps simultaneously into the genital groove. Mating behavior in *Dysdera* and in the mygalomorph spiders follows the same pattern.

The eggs of *Ariadna* are laid in the posterior portion of the tube, without being enclosed in an egg sac. The eggs are not sticky and the female, when disturbed, may move through the egg mass with little difficulty. The very few threads which tie the eggs loosely together may, therefore, be the result of the movements of the female over a considerable period following the laying of the eggs.

Egg masses and young spiders are rarely found with adult females in collections. The difficulty of extracting the entire web intact probably insures loss of some eggs and young even when attempts are made to collect them. Two collections of *A. bicolor* from the Emerton collection in the Museum of Comparative Zoology contain the following notes: "in closed bag with cocoon of about 25 eggs" (one female in this vial), and "with young in tube" (this vial contains two females and twelve young).

Two females of the same species that I collected on Gibraltar Island produced eggs in captivity. Females and offspring were preserved shortly after the eggs began to hatch. With one female were 26 eggs and hatchlings. There were a few more empty chorions than hatchling spiders; apparently a few young were lost even with careful removal from the web. The second female produced 71 eggs, a little more than half of which had hatched at the time of preservation. The remaining eggs, except one, contained well-developed embryos which probably would have emerged. Fresh egg masses, collected with three different females on Gibraltar Island contained respectively 46, 69, and 95 eggs. It is believed that no eggs were lost from these masses during collecting.

Ariadna seemingly has an extended breeding season. There is a distinct tendency for males to be most abundant in late summer, but in Ohio and Pennsylvania, male *A. bicolor* may be collected from late May through September. The relative infrequency of males in most collections suggests that they tend to mature mostly during a short period of time, and may live only a short time after mating. Mature females evidently live more than one season. They may be collected, along with juveniles of all sizes, at almost any time of year. Winter, when the spiders retreat deep into their webs, is a possible exception, but lack of collecting at this season prevents a definite statement.

The chromosomes of one species of *Ariadna*, *A. lateralis* of Japan, have been reported by Suzuki (1952). The diploid number is eight, the smallest known for any species of spider. Sex determination is XO, the male being the heterogametic sex. In view of the tendency to regard high chromosome number as primitive and low numbers as derivative within a given taxon, the chromosome number of *Ariadna* is especially interesting. One species of the Liphistiidae has a 2N chromosome number of 94 or 96. Most araneomorph spiders range between $2N = 24$ and $2N = 36$.

PATTERNS OF SPINATION

The cuticular structures referred to as spines both here and in araneological literature in general, are certainly not spines in the entomological sense of the term. According to the generally accepted definition (Snodgrass, 1935), a spine is an immovable outgrowth of the entire body wall, is lined by epidermal cells, and is not alveolate. The so-called spines of spiders, presumably even the largest of them, are alveolate, hence usually movable, and are secreted

by a single epidermal cell. Therefore they are setae.

Setae of spiders fall into several intergrading categories on the basis of diameter. These are usually referred to as spines, setae, and hairs. The distinctions among these three setal classes are useful and the terms are firmly fixed in the literature. I have continued to use all three words in their araneological senses in preference to causing confusion by the introduction of unfamiliar or newly-coined words.

Most of the leg spines of *Ariadna* are borne on the metatarsi, tibiae, and femora. Occasionally there are one to a few on the patellae. In later instars, spination of juveniles is like that of females. Second instar juveniles have a female pattern of spination, but the number of spines is much smaller than in adults.

Femoral spines in mature specimens of both sexes are limited to the upper surface of the segment, except on the first, and rarely the fourth, leg. Females have, on the distal prolateral surface of the first femur, a single long slender spine. Two species, *A. gracilis* and *A. multispinosa*, have two or three such spines on each first femur (Figure 7). The constancy of these spines is almost one hundred percent in females and in juveniles after the first molt. In males the prolateral spines of the first femur are often suppressed. Usually the spines are still represented by setae that may be set in enlarged sockets or be somewhat spiniform, indicating their homology with the spines of the female.

In both sexes the spines of the upper surfaces of the femora are arranged in three longitudinal rows. One row runs along the dorso-median axis of the femur, the other two along the lateral margins of the upper surface. The cylindrical cross-section of the femur makes delimitation of dorsal and lateral surfaces somewhat ambiguous. All three spine rows have been arbitrarily termed dorsal, although the lateral ones show some tendency to "slip" down onto the lateral surfaces of the femora.

Dorsal spination of the femora is reduced or absent in females but strongly developed in males. In females, retention of a single distal spine of the inner row on femora II and III (in about ten percent of the individuals) represents the lower extreme in spine reduction. A common pattern in females is a distal circlet of three dorsal spines, one in each row. At the observed upper limits in females are found two spines in each of the outer and middle rows, and three in the inner, in a few individuals. The spination of each of the four femora varies in an individual, usually by a reduction in the number of spines posteriad. Occasionally the fourth femur will bear a variable number of spines basally in the middle row.

The number of dorsal femoral spines is highly variable in males both intra- and inter-specifically. The range in the specimens examined was zero to thirteen on a single femur. The majority of the spines are usually in the middle row. The lateral rows often equal each other in spine number.

On the tibia, the ventral spines occur in two rows, which on legs I and II are almost always present in both sexes (Fig. 3); in males, however, the lateral spines occur in one or more rows and are almost always present; if present in females, the lateral spines occur in one row. The dorsal spines rarely occur in males; and a "supernumerary" spine just outside the basal spine of one or both ventral rows in males. Variation in the number of tibial spines is considerable in the genus, but often very slight within a species. In females, lateral tibial spines on the first two legs are usually either present in numbers or almost entirely absent in a given species. The number and arrangement may be variable in a species that has them. Particular patterns are indicated in the species descriptions.

The metatarsi bear a larger and more variable number of spines than the other

podomeres. Only the main features of the variation can be dealt with here. In females on legs I and II, there are two ventral rows of spines, usually with seven to thirteen spines per row (Fig. 13). Metatarsus III also bears two ventral rows, but rarely has more than three spines in the outer and two in the inner row. The fourth metatarsus has a distal comb of spines on the inner ventral surface. This comb is made up of a transverse row of two to eight modified spines set in contiguous sockets (Fig. 31). Elsewhere on the podomere, spines are few or absent. Lateral metatarsal spines occur sporadically in females except on leg III, which usually has one or two prolateral spines.

Metatarsal spination in males is very different from that in females, except on the fourth metatarsal comb, which is alike in the two sexes. The sexual differences in metatarsal spination consist of reduction in the number of ventral spines, and addition of lateral and sometimes dorsal spines in the males.

Male first leg. Of the American *Ariadna*, sixteen males are known. Eleven of these have the metatarsus of the first leg modified in some way. The presence or absence, and the particular form, of this modification furnish the best species characters for the males.

The modified metatarsi are either transversely sinuous or sharply bent (Figs. 41, 51). If sinuous, they are also usually slender, and may bear one or two conical projections. If sharply bent, the metatarsi are thicker and bear one or two lateral projections. In either case, the projections may bear spines (Figs. 32, 33).

In those males that have heavy first metatarsi with lateral projections (apophyses), modified spines occur on the first tibiae. These spines are very short, flat, and wide, and occupy the distal part of the inner ventral row of tibial spines. The number of spines so modified varies from one to three.

DEVELOPMENTAL AND TRAUMATIC CHANGES IN SPINATION

Spination in adults of a given species of *Ariadna* is slightly to moderately variable, depending upon which surface of which podomere is considered. The maximum variation noted in a single character (the number of spines in the ventral rows on metatarsus I) was plus or minus five from the range midpoint. The minimum was minus one spine (first femur, prolateral) where the modal number was one. In this case, variation was quite rare. Of the total number of spine characters, about twenty percent fall into the category of slightly variable; that is, their constancy is ninety percent or more. However, among several hundred adult *Ariadna* examined, not one specimen had a completely symmetrical spination, and no two specimens had the same spination.

The question of the basis of this variation immediately arises, especially because at least some characters appear to be under rather strict genetic control.

Comparison of young specimens of *A. bicolor* with adults of the species provides a partial answer to this question. Five broods of young were available produced from eggs laid in captivity. The spiderlings were known to be in the second instar. One brood was from Massachusetts, two were from Ohio, and two from Florida.

Ariadna, as other spiders, hatches from the egg as an unpigmented spiderling without hair, setae, or spines. It molts almost immediately upon freeing itself from the chorion. The second instar is provided with setae and spines, which may be less well differentiated from each other than they become later. In all five broods of *A. bicolor*, not only was every individual symmetrically spined, but each was spined exactly the same as the others, with one minor qualification: occasionally one of the spines was so slender that it resembled the irregularly arranged setae. However, its position indicated its nature clearly.

All spines at this state are relatively much slenderer than in the adults.

The second instar leg spines of *A. bicolor* consist of two rows of three each on the ventral surface of tibia I, an outer row of three and a single inner spine on the ventral surface of tibia II, a single ventral spine on metatarsus III, two spines in the comb on metatarsus IV, and a single prolateral spine on femur I.

The spination characters showing the greatest constancy in the adults are present in the second instar in almost their final number. The addition of only one spine to each of the ventral tibial rows and one to the metatarsal comb produces the spine number found in 90 percent or more of the adults. The prolateral spine on femur I remains single.

The addition of these spines almost always takes place at the second or third molt, after which, in these particular characters, there is usually no further change with subsequent molts. No statistically significant change in any feature of spination occurred during the last molt in the few samples examined for such a change.

The ventral spine rows of metatarsi I and II are the most variable of the spination characters. There appears, however, to be a fairly regular pattern of addition of spines. The second instar, as noted above, has three spines in each of these rows. In the adult, the proximal and distal spines, and the one at the middle of each row, are of about equal length and are much longer than the others. These long spines are believed to be the original three found in the second instar. Between these "primary" spines are others of varying lengths.

In general, the distal spine in a series between two primaries is the longest, and the lengths of the others gradually diminish proximally until the next primary is reached. Sometimes there may be a long "secondary" spine interrupting the series, breaking the series into two shorter ones that repeat the same pattern (Fig. 13). I believe that the length of a spine is an indication of the molt at which it appeared, and that rearing of a few species will reveal enough of the pattern of addition of spines to allow aging of specimens on the basis of their spination.

The uniformity of juvenile spination suggests that the genetic basis of spination in *Ariadna* is either subject to little variation or is highly canalized, and that the variability in adult spination should be attributed largely to developmental "accidents." Until large-scale rearing of *Ariadna* has been carried out, little can be said about the effect of environmental conditions on development and variation of spination. A few observations derived from preserved specimens are of interest, however.

Differential expression of a particular spine pattern is obvious in preserved material, and is of frequent occurrence. It is most noticeable in males. The number of spines in the ventral metatarsal rows of males is small, usually two or three spines per row, as compared with six to twelve or more in the females. In the wide spaces between the spines of the male, setae with slightly enlarged bases and sockets often occupy the spots where the spines of the female would be. The male pattern of spination on this segment may perhaps represent a suppression of the spines that have been added since the second instar, but the suppression is not necessarily complete.

The same sort of effect is occasionally observed in females. A spine row that "should" contain four evenly spaced spines may have a conspicuous gap in it. Standing in the gap may be a seta which corresponds to the missing spine. The phenomenon in both sexes suggests that, if we had any knowledge of the genetics of *Ariadna*, we might be speaking here of the expressivity of a gene.

In cases such as the above the trichogen cells that produce the spines fail, either completely or partially, to function. There are also cases of overfunctioning or appar-

ent duplication of these cells. In some males, the spines of the first metatarsi or tibiae are greatly thickened or widened as compared with the other leg spines (Fig. 40). Rarely an individual of either sex will be found in which a spine is slightly or deeply bifid at the tip. In a few of these cases the division extends to the base, so that two spines, closely appressed to each other, stand in the same socket. Too little is known of the histology of *Ariadna* epidermal cells to warrant suggestions of reasons for most cases of developmental duplication or multiplication of spines.

Traumatic effects upon spine number are much more easily dealt with. Seizure of an appendage by another organism nearly the size of the spider or larger will usually result in the spider's sharply twisting itself free of the trapped appendage. No reflex autotomy occurs, but there are weak points in the appendages, and breaks at these points seal themselves off rapidly. If an appendage is severely mangled but not pulled off, the spider will itself later break off part or all of the appendage. Provided the animal has at least one more molt in the offing, no sooner than several days after the injury, the lost appendage will be regenerated.

Regenerated appendages are at first smaller and paler in color than the original ones, and customarily have a reduced spination. With each further molt they become more like the unregenerated appendages, but probably rarely catch up with them, except in female mygalomorphs. Although reduction in the number of spines is general in regenerated appendages, the particular pattern assumed by the spines is not very predictable; various irregularities have been observed.

An injury that does not result in autospasy of the appendage heals, leaving a localized scar. If a molt follows, various results may be observed. One specimen I examined had a gap in a spine row with an area of pale cuticle where the spines were missing. Examination of the exuviae of the previous instar of this individual showed a healed wound covering an area which should have borne two to four spines. Perhaps a superficial injury might heal without effect upon spination, but such a result would be difficult to detect in field-collected material.

Of especial interest is a specimen of *A. bicolor*, in which one of the metatarsal rows contained 19 spines, the maximum number for the species otherwise being 12. Near the distal part of the segment, a cluster of half a dozen spines occupied a semicircular area lateral to the rest of the row. These extra spines were oriented in various directions, not extending diagonally down and forward as did the other spines of the row.

Probably a small wound lateral to the spine row had occurred in an earlier instar. The multiplication of trichogen and tormogen cells, and their migration to the wound area during healing, would result in the production of supernumerary spines in an abnormal location. Wigglesworth (1954) describes the experimental production of this effect in the hemipteran *Rhodnius*.

In summary, then, it appears that a large portion of the variation in spination in adult *A. bicolor* is produced by transient or local physiological changes, including trauma. The extent to which varying environmental conditions might produce a harmonious variation of the spine pattern is unknown.

SPECIATION IN THE GENUS *ARIADNA*

To be able to point out lines of evolution among the American *Ariadna* that could be supported by considerable evidence would be gratifying. Unfortunately, this does not yet seem possible. Because of the paucity of material of many species and the morphological and ecological conservatism of the genus, differences are relatively few and slight in most cases. Morphologically, any one of the American species

could probably have given rise to any of the others. Nevertheless, some possible relationships are apparent. It must, of course, be borne in mind that the following discussion is quite tentative and may require extensive change when more material becomes available.

Three groups of species are moderately well defined. Not all of the species fit into these groups, and the placement of some species in the groups is ambiguous.

The *bicolor* group includes a series of species that occur from North America through Mexico, in the mountainous portions of western South America, and on several islands adjacent to the Mexican or South American mainlands. In this group are the widespread North American *A. bicolor*, *A. pilifera* of the U. S. and Mexico, *A. pragmatica*, *A. weaveri*, *A. caerulea*, *A. cephalotes*, *A. murphyi*, *A. peruviana*, and *A. maxima* of Chile. Two other species, *A. isthmica* from Central America and *A. tovarensis* from Venezuela, may belong here also.

Five of these species are grouped together by one of the more satisfactory of the Mahalanobis' distance analyses, shown in diagram 7 of Beatty and Bossert (in prep.), and other methods of analysis associate several of them. Although *A. bicolor*, *pragmatica*, and *caerulea* are placed further from the above group than most other species, they decidedly belong in the group. *Ariadna bicolor* is actually quite similar in both sexes to *A. pilifera*. The distinctions between the species are primarily the increased numbers of spines on most appendages in the females of *A. pilifera*. The modifications of the male first metatarsi are very much alike. (Male characters were not included in the calculation of Mahalanobis' distance.)

The elevational range inhabited by these species is almost totally unknown except for *A. bicolor*, recorded from near sea level to 7000 feet (0–2130 m), and *A. pilifera*, taken from about 2700–7500 feet (800–2300 m). It appears likely that this species group represents a diversification of a stock that was distributed throughout temperate North America and the mountainous areas of South America. Independent migrations from various parts of this range are the probable origins of *A. pragmatica* on islands in the northern Gulf of California, *A. weaveri* on Clarion and Socorro Islands, *A. murphyi* on the Chinchas Islands off Peru, and *A. maxima* on the Juan Fernandez Islands.

The central American *A. isthmica* and Venezuelan *A. tovarensis* are somewhat similar to the members of the *bicolor* group, but apparently occur primarily in tropical lowlands, and are only doubtfully to be included in this group

All eleven of the above species are characterized by the presence, in the females, of two ventral rows of four spines each on the first tibiae, and an outer ventral row of four spines on the second tibiae. The inner ventral row on the second tibiae contains two spines in *bicolor*, *pilifera*, *pragmatica*, and *weaveri*, the northernmost members of the group; three spines in *cephalotes* of Colombia and Ecuador and *tovarensis* of Venezuela; and four spines in the other members of the group. The metatarsal comb contains two spines in *murphyi* and *pragmatica* (both island-inhabiting species); three in *bicolor*, *weaveri* and *peruviana;* and four in the remaining species. Only modal numbers are given for these characters. Except for *pilifera* and *caerulea*, however, there is relatively little intraspecific variation in the characters.

Male characters, as far as they are known, show some agreement with this grouping. Of the four American species that have prominent spurs on the first metatarsi and enlarged spines on the first tibiae, three, *bicolor*, *pilifera*, and *peruviana*, are in the *bicolor* group. The fourth species showing these modifications, *gracilis*, is morphologically far removed from most species of the genus. It is obvious, however, that the male leg modifications

and the female spination are not strongly correlated with each other. The other eight members of the *bicolor* group include males with sinuous first metatarsi without spines and others with unmodified metatarsi that are entirely spineless. Grouping of the species on the basis of male characters produces a similar heterogeneity of female spine patterns within each group.

The *arthuri* group includes *A. arthuri*, widespread on islands in the Caribbean, *A. multispinosa* in Hispaniola, and *A. tarsalis* in the Galapagos Islands. In these species, the first and second tarsi have more than four spines in each ventral row. The modal number for each row in *arthuri* is six. Too few specimens of the other species are known to establish a meaningful mode, but the observed range is four to nine in *tarsalis* (three specimens) and eight to eleven in *multispinosa* (two specimens). All but one of the specimens of the latter two species are immature. Only two other species show a similar tibial spination: *tubicola* from Venezuela and *gracilis* from the Amazon Basin. Both of these species are rather strongly divergent from the rest of the genus. The only affinities either of them show are weak ones with the *multispinosa* group.

The *multispinosa* group appears to be distributed on the Caribbean and Galapagos Islands with further speciation on Hispaniola. Since, in spite of their sedentary habits, *Ariadna* species are quite successful colonizers of new territory, one might expect a mainland member of the group to occur in Mexico or Central America. Prior occupation of this area by other species of the genus would, of course, reduce the possibility of such an occurrence. In fact, however, a single mature female collected by me in northeastern Mexico near Monterrey appears to be a new species of the *multispinosa* group. Because only one mature and a few juvenile specimens are on hand, the species has not been described. No other species from North or Central America resembles the *multispinosa* group in spination.

In this group, *arthuri* and *tarsalis* each have two spines in the metatarsal comb, *multispinosa* has four. It is curious that, of the five American species in which the comb contains only two spines, all but *obscura*, from eastern Brazil, inhabit islands. Two other island species, *weaveri* and *peruviana*, have three comb spines, *solitaria* has four.

The third species group centers around *A. mollis* of southeastern Brazil, Uruguay, and Argentina. Other species of the group are *boesenbergii* and four as yet unidentified species known from the São Paulo and Diamantina areas in southeastern Brazil. The latter four species probably include *A. crassipalpus* Blackwall, *A. conspersa* Mello-Leitão, *A. dubia* Mello-Leitão, and *A. spinifera* Mello-Leitão. In the absence of type specimens, it has so far proved impossible to assign the available specimens to any described species. They may not all belong to the *mollis* group, but certainly most of them do. According to the computer analysis, *A. boesenbergii* and, to a smaller extent, *A. mollis* link the *mollis* and *bicolor* groups.

Ventral spination of the first two tibiae in the *mollis* group is generally like that of the *bicolor* group. The metatarsal comb contains four or more spines in all members of the *mollis* group. Both sexes of *mollis*, *boesenbergii*, and two of the unidentified species, are known. In all of these, the carapace and abdomen are predominantly light in color, and in *mollis* and *boesenbergii*, there is a conspicuous pattern of light and dark bars on the abdominal dorsum. It is impossible to be sure whether the unidentified species referred to above did or did not have a pattern in life. The pattern can be destroyed by poor preservation.

The material of the other possible members of the group consists of two distinctly different males, one from Diamantina and one from São Paulo, and several females

from São Paulo. It is not possible to match either male with the females with any acceptable degree of probability. The females are all very dark in color, in contrast with other members of the group. They may belong elsewhere.

It appears possible that the La Plata River may have acted as a barrier permitting differentiation of an originally single stock into *A. boesenbergii* to the north and *A. mollis* to the south. Later migration would then result in the observed occurrence of both species on both sides of the river at the present time. Too little is known of the actual present distribution of either species, however, to do more than point out the possibility. Mello-Leitão cited the occurrence of both species at several localities not shown on the distribution map (Map 2) but, since he once incorrectly synonymized the two species, his identifications cannot be relied upon.

This genus presents more interesting problems in the area occupied by the *mollis* group than it does anywhere else in the Americas. Of these problems, the nomenclatural difficulty is the most obvious, but least interesting. Once the Mello-Leitão types become available, the proper names should be easily assignable to the specimens.

Of much greater interest is the fact that, in all of the Americas, only in the area from southern Brazil to northern Argentina is there definite evidence of sympatry of two or more species of *Ariadna*. A collection from Diamantina contained a male of *A. boliviana* and one of the unplaced males mentioned earlier. Another collection taken in Buenos Aires contained two female *mollis* and two female *boesenbergii*. Collections from the immediate vicinity of São Paulo include at least three and possibly four species, none as yet identified.

Field study of the microhabitat choice and general ecology of *Ariadna*, especially in the São Paulo region, should provide data on division of habitat and might suggest some reason for the allopatry of most American species. In general, a given species of *Ariadna* appears to be able to tolerate a wide range of climatic conditions as long as its preferred microhabitat is available. As a result, most species have an extensive geographic range, unless they occur on islands. Even one island species, *A. arthuri*, ranges over a large area (Map 4). How four species of these spiders, conservative as they appear to be in choice of microhabitat, can occupy a small area simultaneously is at present a seemingly insoluble puzzle.

The occurrence of *mollis* and *boesenbergii* together, apparently at a single collecting site, is of interest for a further reason. A single vial received from the Museo Nacional de Ciencias Naturales in Buenos Aires contained two females of each species. All four specimens had been identified as *A. mollis*.

Although it is difficult to assess the degree of similarity or difference in such a generally uniform genus, to the naked eye, *mollis* and *boesenbergii* are certainly very similar in appearance. They are the only two species of the genus with a conspicuous abdominal color pattern, they are of about the same size, and they show no more than an average number of differences from each other in spination. Although they may not be the most similar pair of species in the Americas, they are not far from being so. This is exactly the reverse of the phenomenon of character displacement which has gained considerable attention recently. (I might add that I have yet to see any strong evidence for the occurrence of character displacement in any spider species. It must be admitted, however, that no one has made a careful search for it.) Whether any sort of behavioral or ecological displacement occurs in these species is not known.

The remaining species, not placed in any of the above groups, are either divergent from the three described groups or are at the moment unplaceable. Three of them, *boliviana*, *obscura*, and *solitaria*,

may be related to the *bicolor* group. However, only a single female of *obscura*, one juvenile of *solitaria*, and one female and two males of *boliviana* have been seen. Without more material, I prefer to leave them unassigned.

Three species, *tubicola* from Venezuela, *gracilis* from the Amazon Basin, and *fidicina* from the Pacific Coast of North America, are the most divergent of the American species. Except for some possible connection of *gracilis* with the *multispinosa* group, none of them is similar to any other American species (as close similarity goes in this genus). It is especially unfortunate that among these three species, both sexes are known only for *A. gracilis*.

No further speculation on the evolution of *Ariadna* in the Americas appears worthwhile at present. Until the Old World fauna of the genus is revised, and much more collecting has been done in the southern hemisphere where many undescribed species probably exist, no reasonable phylogeny can even be suggested, much less defended. Study of the ecology and behavior may provide clues to the evolutionary history of the genus, but if the animals are as uniform in these characters as they are in morphology, solution of the problem will be difficult.

TAXONOMIC CHARACTERS IN HAPLOGYNE SPIDERS WITH PARTICULAR REFERENCE TO THE GENUS *ARIADNA*

The haplogyne spiders (Haplogynae) include the families Plectreuridae, Diguetidae, Scytodidae, Sicariidae, Dysderidae, Caponiidae, and Oonopidae. They are two-lunged or lungless spiders with simple external genitalia. This simplicity is regarded as primary and primitive. Palpi of the males lack hematodochae, the inflatable membranes that expand the palpal organ, and often consist of a simple globose bulb that tapers to a spinelike embolus. In a few families (e.g. Diguetidae, Dysderidae), the bulb may be subdivided, with a conductor, but the palpal organ never approaches the complexity usual in higher araneomorph spider families. The female has a patch of slightly differentiated cuticle in the genital area, but other external genital structures are either absent or consist only of shallow depressions.

For about 100 years, araneologists have relied heavily upon external genitalia for distinguishing among species of spiders. The genitalic simplicity of the haplogyne families sharply reduces the usefulness of the genitalia as specific characters. The taxonomy of haplogyne spiders, and of mygalomorphs (orthognaths), which also have simple genitalia, has therefore been considered difficult, and has been relatively neglected until recently.

In descriptions of haplogyne spiders, a wide variety of specific characters has been used. The palp of the male, sometimes the genital area of the female, the spermathecae of the female, the number and arrangement of the eyes, the number and dentition of tarsal claws and cheliceral teeth, the shape of the sternum, the length and proportion of the legs, and the spination of the appendages have each been described by one or several authors as being distinctive of certain species.

Heretofore, no attempt has been made to determine the range of variation of "diagnostic" characters within populations of a species, or, at least, the attempt has not been reported. The validity of many species is therefore questionable.

METHODS

Examination of the genus *Ariadna* for usable taxonomic characters involved several steps. The literature was searched, and a list of diagnostic characters employed in the genus was drawn up. Next, specimens of several species were examined for the possible existence of additional characters that had not previously been used taxonomically. With an extensive list of characters prepared, numerical data for

each specimen were recorded, and the results were analyzed to determine whether they would provide statistically significant characters.

In published descriptions of *Ariadna* species, almost every external feature has been described at least once. The selection of characters by a particular author seems, however, to have been based only on whatever happened to strike his eye. Only occasionally have supposedly diagnostic characters been pointed out, and uniformity, system, and completeness are absent. Often the characters are reported incorrectly. Bryant (1948), Chamberlin (1916), Mello-Leitão (1916, 1947), Petrunkevitch (1926), and Simon (1891, 1893a) all reported that the fourth legs, in species of *Ariadna* they described, were entirely spineless. Examination of hundreds of *Ariadna* specimens, including types of species described by the authors cited, reveals that the fourth leg is never spineless in *Ariadna*, except in very small juveniles, and even there only rarely. This mistake led to an erroneous statement in Chamberlin's diagnosis of *A. murphyi* (1920) in which he states "metatarsus IV, armed at distal end of leg instead of leg IV being wholly unarmed."

Various authors (Blackwall, 1858, 1863; Mello-Leitão 1917; Petrunkevitch 1929) have described the chelicerae as being without teeth, or have given an incorrect number of teeth. Again, the descriptions were shown to be in error by examination of one of the specimens seen by these authors, and by the constancy of the number of cheliceral teeth in many other specimens.

It was also common practice to describe the ventral spination of the first and second tibiae and metatarsi as consisting of some number of pairs of spines. The spines are, in fact, not arranged in pairs, but in two distinct longitudinal rows (Fig. 13). The two rows often do contain the same number of spines, but more often they do not. Even when the two rows are equal in spine number, the spines are not always opposite each other. The only notation of spine position that proved satisfactory in this study was one based on the potential presence of one to four longitudinal rows of spines on each of the leg surfaces (see p. 438).

The examination of specimens revealed no new categories of characters, but it did show that many more characters were available than had previously been used in descriptions of new species. The inaccuracy of many such literature reports was clearly demonstrated. The list of characters ultimately settled on for intensive investigation and statistical analysis included the entire spination of the appendages, the cheliceral teeth, and a series of measurements. Other characters were omitted as being unsuited for statistical treatment.

Data were recorded on IBM cards and analyzed by the IBM 7094 computer at the Harvard Computation Laboratory. Methods and results of the analysis are discussed in a separate paper (Beatty and Bossert, in prep.).

ASSESSMENT OF THE CHARACTERS

For data on intraspecific variation in these characters, see Tables 2 to 23.

The number of cheliceral teeth proved to be a generic character. All species of *Ariadna* normally have three teeth on the promargin and one on the retromargin of the fang furrow. Variation from these numbers is infrequent.

Spination of the palpal patella, ordinarily the presence of one spine as opposed to the complete absence of spines, was a useful character in many instances. There is a small to moderate amount of variation, usually not bilateral. A small series of specimens would be sufficient to show the normal condition in all species. The spines of the tibia and tarsus of the palp are highly variable in number. Only occasionally was the difference between two species

significant, and even then only unilaterally. Ranges in spine number on these segments usually overlap to such an extent that they are unusable as specific characters.

The spines of the first two legs present most of the useful taxonomic characters to be found in the spination of the genus. The femur of most species bears one large prolateral spine. Variation of this character in females and juveniles is virtually absent. (In males the spine is often suppressed.) Two species, *A. gracilis* and *A. multispinosa,* have two or three spines in this position. Dorsal femoral spines are normally either present or absent. Normally spineless species may have one dorsal spine, species normally having spines usually have two to four. Overlap of the range is rare. The presence or absence of prolateral and retrolateral spines on the tibiae is a very useful character. In species having lateral spines on these segments, difference in the number of spines is usually not helpful.

Ventral spination of the tibiae is an excellent character, particularly that of the inner ventral row of the second tibia. With respect to the basic pattern of spination on this surface, there are two groups of species: in the first group the maximum number of spines in all rows is normally four, in the second the minimum is normally five. In most species of the first group, the variation is only slight, but in *A. pilifera* and *A. caerulea,* it is considerable. Among the species in the second group, the number of spines per row is much less constant. In all species, the inner ventral row on tibia II is least variable within a species, and it also shows considerable interspecific variation. The ventral rows of spines on the metatarsi usually have the widest range of variation of any spination character. Nevertheless, given a small series of specimens, they provide useful supplementary characters at least for species that fall near the ends of the range of intrageneric variation.

Most spine arrangements of the third leg are not taxonomically useful. The ventral and lateral spines of the metatarsi are the most constant intraspecifically, but the range of interspecific variation is slight. Ventral spines of the tibiae are more variable intraspecifically, and also show a small range of variation from species to species. No character derived from the spination of the third leg can be considered often useful.

The spination of the fourth leg, although denied existence by many authors, does provide one very useful character: the number of spines in a peculiar comb found on the inner ventral surface at the distal end of the metatarsus. This comb contains two spines in some species, three in a few others, four in many, and more than four in a few. Variation is slight, again with the exception of *A. pilifera* and *A. caerulea.* One or two spines are often present in an outer ventral row on metatarsus IV. Other spines of leg IV are usually dorsal or retrolateral on the femur, or ventral on the tibia; their occurrence is sporadic.

The differences in measurements almost all resolve themselves into differences in overall size. The proportions of body and legs are remarkably constant throughout the genus. Here and there a species shows a distinctive feature, such as the relatively long narrow carapace of *A. maxima* or the short distal podomeres of *A. tubicola,* but, in general, a description of the proportions of one species would suffice for most of the others. A certain tendency exists for species that are closely similar in size to be quite distinct in spination and vice versa.

The distance from posterior median to posterior lateral eyes, expressed in diameters of a posterior median eye, has been used rather extensively as a species character by earlier authors. There certainly are interspecific differences in this character, but so many variables are involved in assessing it that its use is very difficult. The eyes are so small that obtaining an accurate measurement is not easy at best,

and a slight difference in the angle at which the observed specimen is positioned under the microscope makes a great difference in the distances being measured. Even with careful measurement, it was found that the intraspecific variation is considerable as compared with that mentioned in published descriptions. I have felt that some use of this character should be possible, because the differences between some pairs of species are striking to the eye. Thus far, however, no generally satisfactory method of describing the character has been found.

Characters not included in the statistical analysis are the following.

Color was often described at length by early araneologists, and was used as a diagnostic specific character. But the hue, being likely to vary rather extensively within a species, is not especially reliable, whereas the pattern of coloration may be. In *Ariadna*, three groups of species are distinguishable on the basis of hue and pattern. One group is composed of species of light coloration, the abdomen ranging from whitish to yellow-orange, the carapace from yellowish to deep red-orange. A second group is dark, with the abdomen purplish gray to dark brown, the carapace brownish or deep mahogany to almost black. Neither of these groups shows any distinctive color pattern on the abdominal dorsum. The third group contains a few species having a distinct dorsal abdominal pattern of yellow transverse bars on a purplish gray or brown background (Fig. 1).

Only the abdominal pattern is consistently usable as a diagnostic character. Color variation is extensive in many species, sometimes, although rarely, to the degree that an adult individual of a normally dark species may be of a light color. The first instar young are, of course, unpigmented, and darken gradually as they mature. Newly molted individuals are whitish, and darken over a period of days.

In a few species of *Ariadna*, dark annuli are present on the legs. These seem normally to be constant, although the number of specimens on hand is relatively small. The presence or absence of these annuli will quite likely prove to be a useful diagnostic character.

The density, length, and color of the pilosity have been used in *Ariadna* taxonomy. They can, under the proper circumstances, be helpful, but are too variable to be diagnostic. Further, their proper use requires recently collected specimens, preferably ones which have molted only a short time prior to collection. In the normal activity of the spider some of the hair may be lost, and in preserved specimens the hair is often almost completely rubbed off, especially from the legs.

In his description of *Ariadna pilifera*, O. P.-Cambridge (1898) said, "Behind the posterior extremity of the sternum, between the coxae of the fourth pair of legs, is a small but distinct shining reddish brown chitinous plate of a truncate conical form, apparently beneath the connecting pedicle; on each side of it is a small oblique slit or orifice (perhaps spiracular openings?) The shape of this plate is probably a good specific character." The plate referred to is a ventral sclerite of the pedicel. It is of no taxonomic use, its shape being practically invariable from one species to another. Portions of the sclerite are often partially covered by folds of the thin adjacent cuticle. These folds may have produced the appearance of lateral slits noted by Cambridge. I failed to find any such slits. Accurate observation of the shape of the sclerite is hindered by the cuticular folds, and efforts to uncover it are likely to damage the specimen.

The structure of the male palp is quite useful in distinguishing species of *Ariadna*, even though it may not always be completely diagnostic in itself. The differences of greatest importance are the size of the organ relative to the size of the spider, and the length, thickness, and curvature of the embolic portion. The palp

is more effectively described by drawings (Fig. 12) than it is in words; its generally small size and the helical curvature of the embolus make accurate and consistent measurement of a series of specimens almost impossible. Proportions of the palpal organ do not present noticeable intraspecific variations, but the small number of males of most species in collections has prevented any significant study of variation.

The metatarsus of the first leg of the male is perhaps the best single diagnostic character found in *Ariadna*. It shows striking interspecific variation in diameter, curvature, spination, and possession of apophyses (Figs. 20–23, 50). The intraspecific variation shown by the only adequate sample of males (*A. bicolor* from Pennsylvania) does not affect the overall appearance of the metatarsus. Unfortunately, males of only about half the American species are known.

The female has no epigynum, there being only a shiny, brownish, somewhat elevated patch of cuticle in the genital area. The internal genitalia present no usable taxonomic characters. There is a single median "seminal receptacle," which probably does not actually receive sperm. Dorsal and posterior to the receptacle is a large membranous bursa copulatrix. Both receptacle and bursa have a uniform structure throughout all the American species.

A TAXONOMIC REVISION OF AMERICAN *ARIADNA*

In spite of the phylogenetic position accorded the haplogyne spiders, the taxonomic problems they present have not, in the past, been fully appreciated or adequately studied. Most araneologists have placed the haplogyne families at or near the base of the araneomorph line. The genitalic simplicity has been viewed as primitive, and other characters are believed to provide supplementary evidence of primitiveness.

If these families are really the most primitive araneomorphs, they offer, in the absence of an adequate fossil record, probably the best material for a study of spider evolution. If the lines of evolution leading from mygalomorph to advanced entelegyne spiders are distinguishable anywhere in living animals, they should be found among the haplogynes. Until very recently the haplogynes have, unfortunately, been among the least known groups of spiders.

During the past several years, revisions of some primarily North American haplogyne families have been published (Gertsch 1958a, b, and c). Currently, Cooke in England and Alicata in Italy are studying the dysderid subfamily Dysderinae, and in America, Chickering is studying the family Oonopidae. But these studies constitute only a beginning of an understanding of haplogyne spiders. The fauna of the south temperate regions has been little examined. There is reason to believe that this fauna, when it becomes well known, may change our ideas of haplogyne classification drastically. Further, the studies mentioned above still rely heavily on genitalia for separating species, although females within a genus of haplogynes may be completely indistinguishable on this basis.

Because of the absence of complex secondary genitalia, araneologists seem to have been at a loss for convenient species characters. The usefulness of characters other than genitalia, eye arrangement, and a few other obvious and traditional features, has been only slightly explored. It must be admitted that some haplogyne spiders actually have fewer external morphological structures than entelegyne spiders, and that identification of females in such genera may be extremely difficult.

The excellent revisions of plectreurids, diguetids, and loxoscelids by Gertsch (1958a, b, and c; 1967) take into account leg length and proportions, spination, size, and eye relationships, in addition to geni-

talia. Even with these additional characters, the genus *Loxosceles* remains a difficult one to deal with. A paper by Cooke (1965b) is the first extensive investigation of non-genitalic morphological characters of haplogynes known to me.

This present study, therefore, has been undertaken not only to provide a much needed revision of the genus *Ariadna,* but also to provide clues to kinds of characters that may prove useful in other genera or families of haplogyne spiders.

METHODS

Measurements. Specimens were measured by the use of ocular grids in binocular dissecting microscopes. A variety of microscopes and grids was used for making measurements, so that neither the magnifications nor the limits of accuracy of the figures are constant. In general, however, the measurements are accurate to about one-tenth unit of the micrometer grid, as is shown by repeated individual measurements. For the larger dimensions, the measurements are accurate to 0.1 mm, for the smaller dimensions to about 0.015 mm. Measurements were made with the specimen in as nearly horizontal a plane as possible, along the lines shown in Figures 5, 8–9, and 15.

A series of 24 measurements of various parts of each specimen was taken. Relatively few of these proved useful in species discrimination (see Beatty and Bossert, in prep.). The range and mean for total length, carapace length and width, and sternum length and width are given in the species descriptions.

Figures and descriptions. The color descriptions are based upon alcoholic specimens, collected as recently as possible. Comparison of old museum specimens with living specimens of the same species shows that *Ariadna* generally retains its color well in alcohol, provided the initial preservation was properly done. The carapace and appendages change color very slightly and slowly, if at all. The abdomen is the most sensitive to improper preservation, and the most likely to change with increasing length of time in preservative. Well-preserved specimens that have not been allowed to dry and have not undergone shrinkage of the soft parts away from the cuticle do not differ noticeably in color from living specimens unless they are quite old (fifty years or more).

Illustrations were made with the aid of a camera lucida, usually at a magnification of 12× or 20×. In most cases only line drawings are presented. Color patterns are present in few species of *Ariadna.*

A few drawings are presented to show the general appearance and structure of the genus (Figs. 1–7, 11–14). Structures of the cephalothorax and appendages of the females are so uniform that there is no reason to present drawings of these parts for each species. Similarly, the female genitalia have not been useful in distinguishing species. The illustration given for one species (Fig. 14) serves equally well for all others. Two views of the male palpi are shown, from the prolateral and retrolateral aspects. The first metatarsus and tibia of the males are illustrated in dorsal view. Hair coverings are omitted from most drawings.

Records. For most species few specimens were available and all records are given. For the United States, locality records are listed alphabetically by state, and counties of the states are also listed alphabetically. Specific localities are given for most species. For the common and widespread *A. bicolor,* only states and counties are recorded.

The major geographical areas are listed in geographic order, beginning in the north. Caribbean islands are listed alphabetically under West Indies. States and territories of Latin American countries are listed alphabetically.

The number of specimens collected at each locality is given. In addition to the ♂ and ♀ symbols used to represent mature

specimens, "o" represents immature individuals. Occasional collectors are named in the text.

Family DYSDERIDAE

Dysdérides C. L. Koch, 1837, Übersicht des Arachnidensystems, vol. 1, p. 20.

Type genus of family: *Dysdera*, Latreille, 1804.

Subfamily SEGESTRIINAE

Segestriinae Simon, 1893, Histoire Naturelle des Araignées, vol. 1, p. 319.

Segestriidae: Petrunkevitch, 1933, Trans. Connecticut Acad. Arts Sci., vol. 31, pp. 333, 365. In this paper, Petrunkevitch raised the subfamily Segestriinae to family rank.

Type genus of subfamily: *Segestria*, Latreille, 1804.

Ecribellate, haplogyne spiders of the suborder Araneomorphae (=Labidognatha). Respiratory system consisting of a pair of book lungs, and tracheal tubes opening through a pair of spiracles just behind the lung slits. Heart with two pairs of ostia. Colulus small but conspicuous, short and wide, bearing several setae. Six spinnerets set close together, short, the anterior and posterior pairs two-segmented, the median pair one-segmented. Anal tubercle wide, and anteroposteriorly compressed. Chelicerae barely united at base only, without apical lamina, normally bearing three prolateral and one or two retrolateral teeth. Labium longer than broad, not fused with sternum. Endites long, parallel, not converging in front of labium. Eyes six in three diads, the anterior median eyes lost. Tarsal claws three, the two superior claws pectinate, the inferior claw with a single minute tooth. Female pedipalp with a short claw. Third pair of legs directed forward rather than backward as with most other spiders. Legs and body covered by fine long hairs, appressed to nearly erect on the body, often erect and forming a conspicuous fringe on the anterior legs. Tarsi and metatarsi often scopulate, especially in males. Rows of setae or heavy spines on the legs, especially on the two anterior pairs. Female copulatory organ much like that of the Diguetidae and Plectreuridae, with large membranous bursa copulatrix, and a single median sclerotized structure that is probably homologous with the seminal receptacle of other spiders, but does not appear to function as a site of sperm storage. Male palpal organ a simple pyriform or long-conical bulb with a spinelike embolus, lacking any accessory structures.

Kaston (1948, 1952) followed Gerhardt and Kästner's (1938) arrangement of spider families, with some modifications, mostly the splitting of various families. This increase in the number of families was largely due to the work of Petrunkevitch (1933, 1939), and included the separation of the dysderids into Dysderidae and Segestriidae. Cooke (1965a) apparently follows this scheme also. He states: "The family is divided into four tribes: Dysderini, Harpactini, Orsolobini, and Rhodini." No segestriine genus is mentioned in his enumeration of genera of the family. Other araneologists, Bonnet (1955) for example, have continued to include the segestriines in the family Dysderidae.

The subdivision of the family was discussed by Petrunkevitch (1933) in the following words: "It seems to me now, however, more reasonable to elevate the subfamily Segestriinae to the rank of a family. They have many characters differentiating them from their nearest relatives, the Dysderinae, such as the position of the third pair of legs, the articulation of the coxae, the arrangement of the eyes. However, the tracheal system is alike in both Dysderidae and Segestriidae."

In his key in the same work Petrunkevitch distinguishes the two families thus:

"Third pair of legs directed forward. Sternum separated from carapace by soft membrane as usual. Eyes in 3 diads. Family Segestriidae.

"Third pair of legs normally directed backwards. Sternum connected with carapace by hard chitin. Eyes in a transverse oval. 3 to 2 claws. Family Dysderidae."

The union of carapace and sternum, by sclerotization of the pleural membrane, occurs in a wide variety of spider families. It is a character common to all members of a family only in the Palpimanidae. From examination of a variety of specimens, it is apparent that whenever a spider becomes heavily sclerotized over much of the body (for whatever the adaptive reasons), one of the first accompanying morphological changes is that the carapace and sternum become fused to each other by sclerotization of the intervening membrane. This feature has been seen in the loricate oonopids, some caponiids, several genera of theridiids, at least three genera of araneids, and some clubionids, in addition to the families mentioned above. These families are presently distributed among three superfamilies. In the oonopids, as in many families, heavy sclerotization is correlated with very small size, in the clubionids and theridiids also with antmimicry, in araneids with apparent protective modifications of the abdomen, and in the caponiids and palpimanids possibly with xeric habitat, although this is a guess. The fusion of carapace and sternum is apparently not a character of much significance at the family level.

The position of the third leg, held forward with the anterior two pairs instead of backward with the fourth, has been considered a unique character of the Segestriidae. Actually the araneid genus *Micrathena* shows this character also and, to judge by preserved specimens, so does the genus *Plectophanes*, variously placed in the Agelenidae or the Toxopidae. Individuals of *Dysdera* and related genera also occasionally rest with the third leg in a position midway between the forward and backward positions, almost perpendicular to the body axis.

By examining Petrunkevitch's own work, and that of Buxton (1913) and Millot (1931), both of whom he quotes, one may find many similarities between dysderine and segestriine spiders. In both groups, in the species examined, the heart has two pairs of ostia, the cephalothorax is supplied with tracheae that originate from the second pair of spiracles, and the thoracenteron is of the simple type.

Buxton (1913) described the coxal excretory glands of various arachnids. He found that mygalomorph spiders have two pairs of glands, which open at the bases of leg coxae I and III. Each gland is made up of a saccule, a collecting tubule, a labyrinth, and an ectodermally lined excretory canal. In the araneomorph spiders, one pair of glands and the collecting tubules are absent, and the labyrinth is considerably simplified.

Variation in coxal glands within the araneomorphs is arranged by Buxton in a sequence from most primitive to most derivative. This sequence begins with the Dysderidae and Sicariidae, in which the labyrinth is a conspicuous loop and the saccule is functional. In most other families examined the labyrinth is present, but the saccule appears to be nonfunctional. Finally, in the Filistatidae, Pholcidae, Theridiidae, and Araneidae, the labyrinth has nearly disappeared so that the saccule and excretory canal are almost directly connected with each other.

The haplogyne genera examined by Buxton included *Scytodes*, *Loxosceles*, *Sicarius*, and *Dysdera*. These genera represent both subgroups of the Dysderoidea, so it is probable that the coxal gland structure is uniform throughout the superfamily.

The alleged difference in coxal articulation does not appear to exist. In both dysderines and segestriines the coxa is open distally across its entire cross-sectional area, and the trochanter articulates with the wall of this terminal opening. Proximally, the articulation of coxa and body wall in both groups is on the dorsal surface of the base of the coxa. The only externally apparent difference between the dysderines and segestriines, with respect to the proximal part of the limb, is that the base

of each coxa and trochanter is more constricted in the dysderines than in the segestriines.

Considering the differences among other spider families, the similarities between dysderines and segestriines are so many, and the differences between them so few and minor that I can find no morphological grounds for separating them at the family level. The possibility that behavioral or distributional information may support their separation can not be denied at present. Until such information becomes available, both groups should remain in the single family Dysderidae.

THE GENERA

The Segestriinae include four named genera: *Ariadna*, *Citharoceps*, *Segestria*, and *Segestriella*. *Citharoceps* of the Pacific coast of North America, and *Segestriella* of South Africa are probably not valid genera, for reasons which will be discussed below. *Segestria*, as presently known, is primarily a Holarctic genus consisting (Bonnet, 1958) of about 25 species. In the Nearctic it is limited to western North America. Seven species are cited as occurring respectively in Madagascar, India, Australia, New Zealand, southern South America, and the Galapagos Islands. The distribution of *Segestria* outside the Holarctic is very poorly known. Quite possibly a number of additional non-Holarctic species remain to be described.

Ariadna is a very wide-spread, but not quite cosmopolitan genus. Approximately 100 species have been described but, of the 41 described from the Americas, only a few more than half are valid, and the same may be true of the Old World species. Few species of *Ariadna* occur in north temperate regions. *Ariadna bicolor*, *A. fidicina*, and *A. pilifera* occur in the United States and Mexico, *A. lateralis* in Japan, and *A. insidiatrix* in southern Europe and northern Africa. The number of species of the genus increases rapidly southward. The largest number of species will probably ultimately be found in the temperate southern hemisphere.

Except by introduction by man, no other genus of the Dysderidae has attained the wide distribution of *Ariadna*. It occurs on all continents except the Antarctic, and on such isolated islands as the Seychelles, New Zealand, the Galapagos, Hawaii, and the Juan Fernandez Islands. As presently known in the Americas, the species of this genus are allopatric, except for a region including southeastern Brazil, Uruguay, and east central Argentina, within which at least six species occur. With more intensive collecting this pattern may change drastically.

Segestriella, described by Purcell (1904), is characterized as "Allied to *Ariadna*, Aud., but differing in having the body elongate cylindrical, the abdomen obtusely produced beyond the spinners, and the fourth pair of legs very short, not reaching hind end of abdomen when stretched out, and with the femur very short and stout, strongly swollen dorsally, the width of the femur between dorsal and ventral edges about 1/2 its dorsal length and almost twice the width of the first femur." These distinctions are simply accentuations of a few characters common to the genus *Ariadna*. Purcell's careful and detailed description of *Segestriella gryllotalpa*, the only species of the genus, shows that it accords completely with *Ariadna* in spine pattern and cheliceral teeth. I have seen no specimens of *Segestriella*, but feel sure that the genus should be considered synonymous with *Ariadna*.

The genus *Citharoceps* of Chamberlin (1924) was distinguished from *Ariadna* solely on the basis of its stridulating apparatus. The files are two patches of coarse transverse grooves which extend along the sloping sides of the cephalic region (Fig. 10). The picks are tubercles at the base of each first femur on the inner surface. In most respects *Citharoceps*

agrees with *Ariadna*, although it is rather divergent in spination and proportions, and is here synonymized with the latter genus. Two species of *Citharoceps* have been described, but they seem conspecific.

Ariadna and *Segestria* have generally been distinguished principally by their eye arrangement (e. g. Comstock, rev. ed. 1948). Because placement of the eyes is often not a constant character within spider genera, Gertsch (pers. comm.) suggested that *Ariadna* and *Segestria* might not really be distinct from each other. However, Simon (1893a) used three other characters in his key to these genera: the shape of the labium, the cheliceral teeth, and the spination of the first pair of legs. Each of these appears to be a significant difference between the two genera. Further differentiating characters are found in the leg and pedipalp proportions, spination of appendages other than the first legs, the shape of the male palpal tarsus, the articulation of the bulb with the palpal tarsus, and the abdominal pattern. Although few Old World species of *Ariadna* have been examined, I consider *Ariadna* and *Segestria* separate and well-marked genera.

Table 1 summarizes morphological characters of *Ariadna* (including *Citharoceps*) and *Segestria*. This summary is based on examination of all the New World species of *Ariadna*, and four species of *Segestria*—*S. florentina*, *S. pacifica*, *S. ruficeps*, and *S. senoculata*. A few specimens of various Old World *Ariadna* and unidentified species of *Segestria* were also examined briefly. The characters cited show a high degree of constancy within each taxon.

Genus *Ariadna* Audouin

Ariadna Audouin, 1825, Explication Sommaire des Planches. *in* Savigny, Description de l'Égypte, p. 109. Type species by monotypy: *Ariadna insidiatrix* Audouin, *op. cit.*, from Alexandria, [Egypt].

Pylarus Hentz, 1827, J. Boston Soc. Nat. Hist., [illegible]:225. Type species by present designation [illegible] *bicolor* Hentz, *ibid.*, from northern [illegible].

Macedonia Hogg, 1900, Proc. Roy. Soc. Victoria, 13:85. Type species by monotypy: *Macedonia burchelli* Hogg, *ibid.*, from Victoria.

Citharoceps Chamberlin, 1924, Proc. California Acad. Sci., ser. 4, 12:607. Type species by original designation and monotypy: *Citharoceps fidicina* Chamberlin, *ibid.*, from Ensenada, Baja California. NEW SYNONYMY.

Segestriella Purcell, 1904, Trans. South African Phil. Soc., 15(3):165. Type species by monotypy: *Segestriella gryllotalpa* Purcell, *ibid.*, from Stompneus, St. Helena Bay, Malmesbury Div., South Africa. NEW SYNONYMY.

Description. Eyes: Six in number, the anterior medians missing. Posterior row of four eyes straight or slightly recurved. Anterior row of two narrower than posterior row. Lateral eyes of each side contiguous. Median eyes contiguous or very narrowly separated. The eyes are thus arranged in three closely spaced diads.

Carapace subrectangular, rounded posteriorly, squarish anteriorly, slightly narrowed at about middle of cephalic region. Head only slightly elevated, thoracic region shallowly depressed laterad of head. Margin of carapace horizontally flanged or slightly upturned, producing a thin, dark marginal line.

Labium one and a half to two times as long as wide, sub-rectangular or sub-hexagonal, distally truncate and usually shallowly notched.

Endites spatulate, medial distal margins (anterior to labium) parallel, tips reaching fang, total length about 1.5 that of labium.

Chelicerae short and moderately tapered. The short fangs are only slightly curved. Anterior cheliceral margin armed with three tiny conical black teeth, the posterior margin with one. The number of cheliceral teeth is probably as constant as a meristic character can be. Of 200 chelicerae examined in one species, one had two teeth on the posterior margin instead of the usual one; there was no other variation. Anteriorly one of 200 had four teeth, and eight of 200 had two teeth. A few of the latter cases were probably ascribable to injury before or damage after collecting.

Table 1. Structural Characters of the Segestriinae

	Ariadna	*Segestria*
Cheliceral teeth	Three anterior, one posterior, all tiny and conical.	Three anterior, two posterior, all triangular.
Labium shape	Short and wide, narrowed at each end. Greatest width near base.	Long and narrow, nearly parallel-sided. Greatest width near middle.
Spination (females)	Tibiae and metatarsi of first two pairs of legs wth two ventral rows of heavy spines, mostly of short to medium length and flattened. Fourth legs with few spines.	Tibiae and metatarsi of first two pairs of legs with two ventral rows of long, slender, nearly round spines. Total number of metatarsal spines on these legs much smaller than in *Ariadna*. Fourth legs with many spines.
Legs and palps	Relatively short and stout.	Relatively long and slender.
Male palpus	Tarsus short, of nearly uniform width throughout its length, notched at tip. Bulb inserted at middle of tarsal length. Palpus similar to that of *Loxosceles*.	Tarsus long, the distal two-thirds much narrower than the basal third, not notched at tip. Bulb inserted over most of the basal third of tarsus. Palpus similar to that of *Scytodes*.
Abdominal pattern	Usually lacking. When present, consisting of transverse bars on a contrasting background. Venter unmarked.	Usually present, some species with a self-colored abdomen. Pattern consisting of a median dorsal longitudinal row of dark lozenges on a light background, plus many scattered small dark spots dorsally and ventrally.

Exposed portion of labrum white, bluntly rounded at tip, reaching to the ends of the endites.

Sternum ovate to sub-rectangular, truncate anteriorly, bearing a narrow pointed articular process opposite the middle of each coxa.

Abdomen longer than wide, usually considerably so, overhanging posterior part of carapace, extending slightly beyond base of spinnerets and anal tubercle, subcylindrical.

Palps short and stout, bearing in females and immatures a pair of spines ventral to the claw, and prolateral spines on tarsus, tibia, and sometimes patella.

Legs relatively short and stout in females, long in males. Order of length 1–2–4–3, or occasionally in some individuals 2–1–4–3, the first and second legs always nearly equal in length. Tarsi obliquely truncate, the pretarsus, bearing the claws, set on the upper surface of the truncation. Superior claws pectinate in a single row, inferior claw short, with a single tiny tooth.

Palp of male with tarsus short and elliptical, bulb pyriform, inserted at middle of length of tarsus. Embolus a simple spine variously curved, usually rather well set off from the bulb.

Female genital area marked only by shiny brown cuticle externally. Internally, a tiny median sclerotized structure probably represents the seminal receptacle. A large membranous sac, corresponding to the bursa copulatrix of plectreurids and dysderines, extends a short distance anterior and far posterior to the epigastric groove. The seminal receptacle has a posterior opening in its somewhat triangular base. From the opening, a short folded blind tube extends forward. A short, curved, pointed tube extends anterodorsally from the base of the receptacle, also ending blindly. The size of this receptacle

alone suggests that it does not actually function as a storage place for sperm. In several mature females, dissection revealed a yellowish white mass in the posterior part of the bursa copulatrix. Probably this mass was sperm. In a discussion of the female genitalia of *Dysdera crocata,* Cooke (1966) stated: ". . . spermatozoa are transferred, not directly to the 'spermatheca' but into the bursa . . . The small proportion of spermatozoa that get into the 'spermatheca' makes it unlikely that the true function of this structure is sperm storage." The female genitalia of haplogyne spiders are in need of further study with a view to elucidating the origin and evolution of the complex epigyna of higher spiders.

Size. Total length varies from 4.0 to 16.0 mm in mature members of the genus, carapace length from 2.1 to 7.7 mm. Leg proportions are rather uniform in most of the American species. Leg I is usually longest, but leg II sometimes exceeds it. The difference between the two rarely exceeds one millimeter and is usually much less.

In females the first leg is about 2.5 times the length of the carapace, leg II very slightly shorter, leg III less than and leg IV slightly more than twice the carapace length. The longer-legged males have leg I about 3.5 times the carapace length, leg II about three and a quarter, leg III about two and three-quarters, and leg IV about two and one-third times the carapace length.

Coloration. Color in the genus *Ariadna* is generally dull, ranging from yellowish through reddish orange and mahogany to a deep brown that appears black to the naked eye. The extent of tanning of the cuticle is probably the chief determiner of color of the carapace and appendages. In only a few species does the abdomen bear a distinct color pattern. When present, the pattern ordinarily consists of transverse bars of yellowish on a purplish gray background. By extension of the area of yellowish, the pattern may come to be one of dark bars on a light background. The color pattern in *Ariadna* is never a median longitudinal series of dark lozenges, as is the rule in *Segestria.* The anterior legs are usually of about the same color as the carapace. The other legs become progressively lighter in color posteriad.

Spination. The tarsi, trochanters, and coxae of all legs lack spines in both sexes of *Ariadna.* In only a few species are there patellar spines. The tibiae and metatarsi, especially the first two pairs, bear many spines. Most obvious of these are the two ventral rows of enlarged, flattened, forward-pointing spines. Femora also bear spines, on the dorsal and prolateral surfaces only.

Key To American Species of *ARIADNA*

Males

1a. First metatarsus armed with one or two strong apophyses, or with short thick spines set on low protuberances; metatarsus in dorsal view usually sinuous or strongly bent inward near base (nearly straight in *A. peruviana*). (Figs. 32–33, 39). 2

1b. First metatarsus without strong apophyses or short thick spines; in dorsal view either straight or slender and sinuous. (Figs. 21, 51). 6

2a. First metatarsus without lateral or ventral apophyses, with two or more short heavy spines arising from low protuberances (apophyses never bear heavy spines distally); metatarsus sinuous or nearly straight. (Figs. 32, 39). 3

2b. First metatarsus with one or two large lateral or ventral apophyses, without short heavy spines; metatarsus curved or strongly bent inward at base. (Fig. 38). 4

3a. Heavy spines ventrolateral, opposite each other, one pair just distal to middle of metatarsus, usually a second pair at distal end of metatarsus. (Figs. 8, 26–27, 32). Caribbean from Curaçao to Florida Keys ..... *arthuri*

3b. Heavy spines lateral, not opposite each other, a single pair placed proximal to middle of metatarsus . (Figs. 34–35, 39). Peru. ..... *peruviana*

4a. With a single ventral apophysis which bears an unenlarged distal spine (this

spine is easily broken off). (Figs. 7, 28–29, 33). Amazon Basin ..... *gracilis*

4b. With a pair of lateral apophyses which do not bear distal spines 5

5a. The prolateral apophysis slightly but distinctly proximal to middle of metatarsus, the retrolateral apophysis more proximal; middle pair of ventral spines inserted distal to the apophysis (rarely, the prolateral spine is at the base of the prolateral apophysis); transverse diameter of palpal bulb less than twice the maximum width of palpal tibia. (Figs. 38, 42–43). Southern Canada; Maine to Florida, southern California, and northwestern Mexico. ..... *bicolor*

5b. The prolateral apophysis distal to middle of metatarsus, retrolateral apophysis about at middle; middle pair of ventral spines inserted at bases of apophyses; transverse diameter of palpal bulb twice or more the maximum width of palpal tibia. (Figs. 20, 31, 36–37, 40–41). Arizona and Mexico. ..... *pilifera*

6a. Metatarsus I straight in dorsal view 7

6b. Metatarsus I slender and sinuous in dorsal view. 10

7a. Abdomen with a distinct dorsal pattern of transverse bars. 8

7b. Abdomen unicolored, or with color marking a broad longitudinal stripe. 9

8a. Patellae of legs I and II each with a prolateral spine; metatarsal comb of leg IV with five to eight spines; midpiece of palp short, about equal to embolic portion in length. (Figs. 1, 16, 17, 22). Southeastern Brazil to Argentina. ..... *mollis*

8b. Patellae of legs I and II without spines; metatarsal comb of leg IV with four spines; midpiece of palp long, much longer than embolic portion. (Figs. 3, 46–48). Uruguay and Argentina. ..... *boesenbergii*

9a. Metatarsi I and II without spines (Figs. 50, 53, 56). Revilla Gigedo Islands (Mexico). ..... *weaveri*

9b. Metatarsi I and II with spines. (Figs. 2, 18–19, 21). Chile, including Juan Fernandez Islands. ..... *maxima*

10a. Embolic portion of palp much longer than midpiece, equal to or exceeding diameter of bulb; midpiece and embolic portion forming about a ninety degree angle with each other. (Fig. 55). 11

10b. Embolic portion of palp equal to or much shorter than midpiece, shorter than diameter of bulb; midpiece and embolic portion forming a relatively shallow angle with each other. (Figs. 44–45, 49). Colombia and Ecuador. ..... *caerulea*

11a. Without dorsal spines on femora I and II. (Figs. 23–25, 30). Central America. ..... *isthmica*

11b. With dorsal spines on femora I and II. (Figs. 51–52, 54–55). Bolivia and southeastern Brazil. ..... *boliviana*

Females

1a. Dorsal spines absent from femora I and II in 80% or more of individuals, remaining 20% usually with only one spine on each of these femora (rarely two or three spines). 2

1b. Dorsal spines present on femora I and II in 90% or more of individuals, usually four or more spines on each first femur, and two or more on each second femur. 10

2a. Comb of metatarsus IV with two or three spines; ventral tibial spines 4–4 on leg I, 4–1 or 4–2 on leg II. 3

2b. Comb of metatarsus IV with four or more spines; ventral tibial spines of leg I 4–4 or more, of leg II various combinations from 4–0 to 5–7. 5

3a. Comb of metatarsus IV with two spines; Patos Island and Cedros Island, upper Gulf of California, and coast of Sonora. ..... *pragmatica*

3b. Comb of metatarsus IV with three spines. 4

4a. Metatarsus III with one inner ventral spine (95%); third tibia with no prolateral spines (90%); posterior median eyes (PME) averaging 1.1 times their diameter from posterior lateral eyes (PLE). United States and northwestern Mexico. ..... *bicolor*

4b. Metatarsus III with two inner ventral spines (78%); third tibia with one or two prolateral spines (70%); PME averaging 1.6 times their diameter from PLE. Revilla Gigedo Islands, Mexico. ..... *weaveri*

5a. Ventral spines of tibia II 4–4 or more. 6

5b. Ventral spines of tibia II fewer than 4–4. 9

6a. Ventral spines of tibiae I and II usually five to seven in each row; comb of metatarsus IV usually with five spines, sometimes with four; tarsi and metatarsi short; anterior legs with purplish gray annuli. Venezuela. ..... *tubicola*

6b. Ventral spines of tibiae I and II usually four in each row; comb of metatarsus IV with four spines; tarsi and metatarsi of normal length; legs without annuli. 7

7a. With prolateral and retrolateral spines on tibiae I and II. Central America. ..... *isthmica*

7b. Without lateral spines on tibiae I and II (except occasionally on retrolateral surface of tibia I in *cephalotes*). 8
8a. Abdomen with a dorsal pattern of transverse bars on a contrasting background. Uruguay and Argentina. ..... *boesenbergii*
8b. Abdomen unicolored dorsally. Colombia and Ecuador. ..... *cephalotes*
9a. With stridulating grooves on sides of cephalic region; abdomen occasionally with dorsal pattern of light bars on a dark background. California and Baja California. (Fig. 10). ..... *fidicina*
9b. Without stridulating grooves on cephalic region; abdomen purplish gray. Colombia, Ecuador, and Peru. ..... *cephalotes*
10a. With either two spines in the comb of metatarsus IV OR two to three prolateral spines on femur I. (Fig. 7). 11
10b. With more than two spines in the comb of metatarsus IV AND only one prolateral spine on femur I. 16
11a. Comb of metatarsus IV with four spines; femur I with two or three prolateral spines. 12
11b. Comb of metatarsus IV with two spines; femur I with one prolateral spine. 13
12a. With lateral spines on tibiae I and II; ventral spines of tibiae I and II five to eight in each row. Amazon Basin of Brazil and Peru. ..... *gracilis*
12b. Without lateral spines on tibiae I and II; ventral spines of tibiae I and II seven to eleven in each row. Hispaniola. ..... *multispinosa*
13a. Ventral spines of tibiae I and II four or fewer in each row. 14
13b. Ventral spines of tibiae I and II five or more in each row. 15
14a. Palpal patella spineless; femur IV with one to three dorsal spines near base. Chinchas Islands off Peru. ..... *murphyi*
14b. Palpal patella with one spine; femur IV without dorsal spines. Eastern Brazil. ..... *obscura*
15a. Tibiae I and II each with one to two retrolateral spines; carapace length 2.0–3.5 mm. Florida and West Indies. ..... *arthuri*
15b. Tibiae I with three retrolateral spines each, tibiae II with none; carapace length 3.7–4.8 mm (see text). Galapagos Islands. ..... *tarsalis*
16a. Tibia II with one to three spines in inner ventral row (100%). 17
16b. Tibia II with four spines in inner ventral row (95%). 20
17a. Dorsum of abdomen with a conspicuous pattern of transverse bars on a contrasting background; comb of metatarsus IV with five to eight spines. Southeastern Brazil to Argentina. ..... *mollis*
17b. Dorsum of abdomen without such a pattern, usually unicolored; comb of metatarsus IV with three to four spines. 18
18a. Metatarsi II and III usually each bearing a retrolateral spine; total number of spines on metatarsus III 10–11. Bolivia and Brazil. ..... *boliviana*
18b. Metatarsi II and III spineless retrolaterally; total number of spines on metatarsus III five to nine. 19
19a. Palpal patella without spines (90%). Southwestern United States and Mexico. ..... *pilifera*
19b. Palpal patella with one spine (83%). Venezuela. ..... *tovarensis*
20a. Palpal patella without spines (100%). 21
20b. Palpal patella with one to three spines (95%). 22
21a. Comb of metatarsus IV with three spines (75%); femur IV usually with one to four dorsal spines. Peru. ..... *peruviana*
21b. Comb of metatarsus IV with four spines (75%); femur IV without dorsal spines. Colombia and Ecuador. ..... *caerulea*
22a. Carapace length 4.2–7.7 mm, mean of 78 specimens 5.97 mm. Chile, including Juan Fernandez Islands. ..... *maxima*
22b. Carapace length 4.2 mm (single immature specimen). St. Vincent Island, West Indies. ..... *solitaria*

SPECIES DESCRIPTIONS

Ariadna bicolor (Hentz)
Figures 38, 42–43. Map 1.

Pylarus bicolor Hentz, 1827, J. Boston Soc. Nat. Hist., 4:225, pl. 2, figs. 3, 4, ♀, ♂. Type specimens from northern Alabama, lost.

Pylarus pumilus Hentz, 1827, *ibid.*, 4:226, pl. 2, fig. 5, juvenile. Type specimens from North Carolina and northern Alabama, lost.

Ariadna pallida C. L. Koch, 1843, Die Arachniden, 10:90, pl. 350, fig. 817, ♀. Female holotype from Pennsylvania, not seen.

Ariadne rubella Keyserling, 1877, Verhandl. der könig. kais. Zool. Bot. Gesell., Wien, 1877:229. Female holotype from Louisiana, New Orleans, in British Museum (Natural History), examined.

A. pennsylvanica: Simon, 1891, Proc. Zool. Soc. London, p. 556, nomen nudum. Simon attributed this name to C. L. Koch, so *A. pallida,* from Pennsylvania, is evidently the species he intended to refer to.

Ariadne mexicana Banks, 1898, Proc. California Acad. Sci., ser. 3, Zoology, 1(7):212. Syntypes from La Chuparosa, Baja California. One in

Map 1

California Acad. Sci. Collection, destroyed. The other in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Ariadna philosopha Chamberlin, 1924, Proc. California Acad. Sci., ser. 4, Zoology, 12(28):606. Female holotype from Isla Partida, Gulf of California, in California Acad. Sci. Collection, examined. NEW SYNONYMY.

Discussion. Although no types of either of Hentz's species exist, the name *A. bicolor* may be assigned with certainty to this species. Specimens from both North Carolina and northern Alabama are available, and are identical with the nearly continent-wide species to which the name *A. bicolor* has been applied for over 100 years. Other species of *Ariadna* are of very limited distribution in the United States: *A. arthuri* in the southern part of peninsular Florida and the Keys, *A. pilifera* in southern Arizona, and *A. fidicina* in the southern half of California west of the mountains.

In spite of Hentz's denial of this fact, his *Pylarus pumilus,* described in half a dozen lines, can be nothing but the juvenile of *A. bicolor,* as suggested by Emerton (1875). Koch's description of *A. pallida* contains nothing distinctive of any particular species of the genus. A large series of specimens from Pennsylvania, the type locality of *A. pallida,* differs in no significant way from other populations assigned to *A. bicolor.*

Ariadne rubella Keyserling, from New Orleans, differs only by its reddish color, according to the description. Some Louisiana specimens are distinctly more reddish than most *A. bicolor,* but are otherwise indistinguishable. In the absence of freshly collected specimens from Louisiana, it is not even certain that the reddish color is natural.

Banks's *A. mexicana* was supposedly distinguishable from *A. bicolor* by its more

slender build and smaller eyes. The former difference does not exist. The eyes are smaller, leaving a much wider space between the posterior median and posterior lateral eyes than in U. S. specimens of *bicolor*, from which *mexicana* does not otherwise differ. This may be a geographic variation, but so few Mexican specimens are available that I do not feel justified in recognizing it even as a subspecies.

Chamberlin's *A. philosopha* from Isla Partida in the Gulf of California has small eyes also. It also occasionally has a prolateral spine on the second tibia, which is extremely rare in *A. bicolor* from other areas. Other differences are well within the range of individual variation of *bicolor*. The spine characters which supposedly distinguish *philosopha* from *mexicana* are much too variable to be so used. *Ariadna bicolor* is so remarkably uniform in most characters throughout the United States that, with additional material, it may become desirable to recognize a subspecies for the Mexican specimens.

Color. Female. Described from a freshly collected specimen from Gibraltar Island, Ottawa County, Ohio. Carapace mahogany, darker in head region. Abdomen purplish gray above and below, with a satiny luster, sometimes slightly iridescent, finely striate with yellow lines. Striations longitudinal on sides of abdomen, transverse ventrally and mid-dorsally. A narrow yellowish lateral line on each side of abdomen, ending at the upper surface of the anal tubercle.

First legs brown to very dark brown, sometimes with an olive green tinge, especially soon after molting. The other legs progressively paler posteriad, the fourth pair light mahogany or dark yellow-brown. Chelicerae very dark brown, almost black. Palps brown proximally, darker distally.

Labium and endites brown, endites with white tips, labrum white. Sternum bright mahogany, margins darker. Spinnerets whitish with pale brown transverse markings. Anal tubercle whitish. Epigastric plates yellowish, ventral surface of pedicel white or translucent. Genital area in the shape of a low wide triangle, slightly swollen, the cuticle brown and shining.

Male. Overall pattern as in the female, but generally paler, the legs and carapace yellowish to medium brown in most cases.

Structure. Dimensions of 80 females: total length 6.1–15.0 mm, mean 8.73 mm; carapace length 3.0–4.8 mm, mean 3.84 mm; carapace width 1.9–3.1 mm, mean 2.40 mm; sternum length 1.7–3.8 mm, mean 2.20 mm; sternum width 1.1–1.6 mm, mean 1.31 mm.

Dimensions of 22 males from a single locality: total length 5.4–7.2 mm, mean 6.15 mm; carapace length 2.7–3.4 mm, mean 2.96 mm; carapace width 1.9–2.4 mm, mean 2.04 mm; sternum length 1.5–2.0 mm, mean 1.75 mm; carapace width 0.9–1.2 mm, mean 1.04 mm. No other collection of males contains more than one to a few specimens. Some of these, however, are larger than any specimen included in the above sample.

Spination. See Table 4.

Diagnosis. The comb of three spines on the fourth metatarsus distinguishes *A. bicolor* from all other New World *Ariadna* except *A. peruviana*, *A. weaveri*, and some specimens of *A. pilifera*. Females may be distinguished from *peruviana* by having only two, instead of four spines in the inner ventral row on tibia II, and from *pilifera* by the absence of lateral spines on the first two tibiae. Females of *weaveri* are quite similar to those of *bicolor*, but are readily distinguished by distribution, and by the characters given in the key. The pair of large lateral apophyses on the first metatarsus of the male *bicolor* separates it from all other known males except that of *pilifera*. The apophyses of *pilifera* are more distal, and the palpal bulb proportionately larger than in *bicolor*.

Distribution. Maine to Florida and west to southern California, Baja California, and northwestern Mexico. Specimens are not

available, however, from large parts of the central plains and the Northwest. The only Canadian records are from two islands in western Lake Erie.

Records. County records only are given for the United States.

CANADA. ONTARIO: Big Chicken Island, Lake Erie, under boards and stones; East Sister Island, Lake Erie, under boards and stones.

UNITED STATES. ALABAMA: *Colbert, Jackson, Madison, Marshall.* ARIZONA: *Coconino.* ARKANSAS: *Benton, Washington.* CALIFORNIA: *San Diego.* COLORADO: *Chaffee, El Paso, Fremont.* CONNECTICUT: *Fairfield, New Haven.* DISTRICT OF COLUMBIA. FLORIDA: *Alachua, Gadsden, Hernando, Highlands, Indian River, Jackson, Lake, Levy, Liberty, Marion, Nassau, Orange, St. Johns.* GEORGIA: *Floyd, Fulton.* ILLINOIS: *Bond, Jackson, Macoupin, Union, Williamson.* INDIANA: *Brown, Crawford, Owen.* KENTUCKY: *Carter, Harding, Madison, Wolfe.* LOUISIANA: *Beauregard, Caddo, East Baton Rouge, Grant, Jefferson, Madison, Orleans, St. Charles.* MAINE: *Knox.* MARYLAND: *Montgomery, Prince Georges.* MASSACHUSETTS: *Barnstable, Essex, Middlesex, Norfolk, Plymouth.* MISSISSIPPI: *George, Hinds, Jackson, Oktibbeha.* MISSOURI: *Boone, St. Louis, Taney, Wayne.* NEW JERSEY: *Cape May, Mercer, Ocean.* NEW MEXICO: county unknown. NEW YORK: *Albany, Bronx, Nassau, Orange, Rockland, Suffolk.* NORTH CAROLINA: *Carteret, Durham, Guilford, Transylvania, Wake.* OHIO: *Ashland, Cuyahoga, Hocking, Mercer, Ottawa, Wayne.* OKLAHOMA: *Comanche.* PENNSYLVANIA: *Blair, Bucks, Franklin.* TENNESSEE: county unknown. TEXAS: *Bastrop, Brazos, Cameron, Comal, Denton, Hays, Kerr, McLennan, Travis, Walker.* VIRGINIA: *Fairfax, Montgomery, Page.* WEST VIRGINIA: *Hancock.*

MEXICO. Isla Partida, Gulf of California, ♀oo, holotype and paratypes of *A. philosopha.* Santa Catalina Island.

Ariadna pilifera O. P.-Cambridge
Figures 20, 31, 36–37, 40–41. Map 1.

Ariadne pilifera O. P.-Cambridge, 1898, Biol.-Cent. Amer., Arach. 1:235, plate 30, figure 9, 9 a-c, ♀. Female holotype from Mexico, Durango, in British Museum (Natural History), examined.

Ariadne comata O. P.-Cambridge, 1898, Biol. Cent.-Amer., Arach., 1:235, plate 30, figure 8, 8a-c, ♀. Female holotype from Mexico, Orizaba, in British Museum (Natural History), examined. NEW SYNONYMY.

Ariadna acanthopus Simon, 1907, Ann. Soc. Ent. Belg., 51:263, figure 5, ♂. Male holotype from Mexico, Guanajuato, in Muséum National d'Histoire Naturelle, Paris, examined. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29: 131; Bonnet, 1955, Biblio. Aran., 2(1):730. NEW SYNONYMY.

Ariadna jaliscoensis Chamberlin, 1925, Bull. Mus. Comp. Zool., 68(4):212. Female holotype from Mexico, Hacienda San Marcos, SW Jalisco, in Museum of Comparative Zoology, Cambridge, examined. Bonnet, 1955, Biblio. Aran., 2(1): 733. NEW SYNONYMY.

Ariadna pilifera: F. O. P.-Cambridge, 1899, Biol. Cent.-Amer., Arach., 2:43; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):732.

Ariadna comata: F. O. P.-Cambridge, 1899, Biol. Cent.-Amer., Arach., 2:43; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 21:131; Bonnet, 1955, Biblio. Aran., 2(1):732.

Not *Ariadna comata:* Banks, 1929, Bull. Mus. Comp. Zool., 69(3):54.

Discussion. This species is much more variable in some normally stable characters than any other American *Ariadna.* For a time it was believed that the specimens on hand might belong to as many as five species. The distributions of these apparent species made no sense, however. With long series of specimens from each of several scattered localities, the variability of the species became evident. This variation is especially pronounced in the population found near Portal, Arizona.

Types of all the species listed in the synonymy above have been examined. The holotype of *A. acanthopus* is a male, the other three are females. Chamberlin's *A. jaliscoensis* differs most from the modal values for characters of other specimens assigned to *pilifera.* In its most divergent

characters, however, the *jaliscoensis* holotype is usually still within the range of variation of other *pilifera* specimens. Only one character, the number of spines on the palpal tarsus, is entirely non-overlapping.

The name *Ariadna comata* was first applied to Central American specimens by Banks (1929), presumably because *comata* was the southernmost species recorded from Mexico. The type of *comata*, when examined, proved to be similar to that of *pilifera*, and quite different from the Central American form. The latter is described herein as a new species.

Color. Male. Carapace dark reddish mahogany. Anterior legs a little lighter, remaining legs yellowish brown. Bulb of palp yellow. Remainder of palp, endites, labium, and coxae yellowish brown, sternum darker. Abdomen purplish gray above and below. Spinnerets and anal tubercle brownish yellow.

Female. Darker than male, the carapace and all legs deep mahogany, becoming almost black on distal podomeres of first leg. Underside of cephalothorax and legs scarcely lighter than upper side.

Structure. Dimensions of eight males: Total length 7.2–10.6 mm, mean 9.15 mm; carapace length 3.8–5.0 mm, mean 4.36 mm; carapace width 2.5–3.1 mm, mean 2.76 mm; sternum length 2.3–3.1 mm, mean 2.74 mm; sternum width 1.30–1.63 mm, mean 1.502 mm.

Dimensions of thirty females: Total length 9.7–15.0 mm, mean 12.02 mm; carapace length 4.9–6.4 mm, mean 5.72 mm; carapace width 2.7–3.9 mm, mean 3.35 mm; sternum length 2.9–3.9 mm, mean 3.33 mm; sternum width 1.55–2.37 mm, mean 1.896 mm.

Male palp. Bulb large, tibia not inflated, the bulb 2.5 times the width of the tibia. Midpiece quite short and conical, embolic portion and midpiece together shorter than maximum depth of bulb. Embolic portion shallowly curved near distal end

Male first leg. Metatarsus strongly bent inward, bearing a large, acute retrolateral apophysis just proximal of the middle and a smaller prolateral one just distal of the middle. Tibia with two to three of the outer ventral spines modified.

Investiture. Male. Hair covering of abdomen rather short. Tarsi of all legs scopulate, metatarsi sometimes with a very short distal scopulate area.

Female. Clothed throughout with conspicuous long hair, normal in pattern of arrangement, but somewhat denser and longer than usual. Color of the hair varies from reddish or brown to black.

Spination. See Table 17.

Diagnosis. The variation in this species makes diagnosis or placement in a key somewhat difficult. The male is closely similar to that of *A. bicolor*. Only in these two species is the first metatarsus stout, strongly bent, and provided with a lateral apophysis on each side. The more distal placement of the apophyses and the proportionately larger palpal bulb distinguish the male of *pilifera* from that of *bicolor*.

In the female of *pilifera*, lateral spines are present on tibiae I and II, separating the species from *bicolor*, which it generally resembles. The ventral spination of tibia II is normally 4–(1–2), and the metatarsal comb usually contains 3–4 spines (three in most populations examined); retrolateral spines are absent from metatarsi II and III and tibia III; metatarsi I and II usually have 7–10 spines in each ventral row, and metatarsus IV usually has 1–2 spines in addition to the comb.

Distribution. Southern Arizona to the Isthmus of Tehuantepec in southern Mexico.

Records. ARIZONA: *Cochise Co.*, Chiricahua Mtns., Portal and Southwestern Research Station, Chiricahua National Monument; Huachuca Mtns., Carr, Ramsey, and Miller Canyons. *Graham Co.*, Mt. Graham near Safford. *Navajo Co.*, 12 mi. S of Show-low. *Pima Co.*, Ajo Mtns.,

Organpipe Cactus National Monument, Alamo Canyon. Baboquivari Mtns., Brown Canyon, and Forestry Cabin; Santa Catalina Mtns., lower Sabino Canyon, Molino Basin, Peppersauce Canyon, Windy Point, Geology Vista, San Pedro Vista; Santa Rita Mtns., Madera Canyon, Roundup Camp.

MEXICO. CHIHUAHUA: Primavera, 5500–6000 ft. COLIMA: 12 mi. E of Manzanillo. DURANGO: Ojo de los Encinos. GUANAJUATO: no further data, o. GUERRERO: Ayotzinapa. HIDALGO: Jacala, Rancho Viejo near Jacala. MICHOACÁN: Jiquilpan, Morelia, Tanci'taro, 6500 ft. MORELOS: Cuernavaca, 3 mi. E of Cuernavaca, 9.6 mi. E of Cuernavaca. NAYARIT: Campostela. OAXACA: 67 mi. NW of Tehuantepec. PUEBLA: Tehuacan. SAN LUIS POTOSÍ: Tamazunchale, 3.8 mi. W of El Naranjo (Veracruz), E of Ciudad del Maiz. TAMAULIPAS: 5 mi. W of Altamira. VERACRUZ: Acultzingo, W of Orizaba, 15 mi. NW of Jalapa.

Ariadna pragmatica Chamberlin
Map 1.

Ariadna pragmatica Chamberlin, 1924, Proc. California Acad. Sci., ser. 4, 12(28):606. Female holotype from Mexico, Sonora, Tepoca Bay, in California Academy of Science, examined. Bonnet, 1955, Biblio. Aran., 2(1):736.

Ariadna scholastica Chamberlin, 1924, Proc. California Acad. Sci., ser. 4, 12(28):607. Female holotype from Gulf of California, Patos Island, in California Academy of Science, examined. Bonnet, 1955, Biblio. Aran., 2(1):737. NEW SYNONYMY.

Discussion. Chamberlin separated his two species, *scholastica* and *pragmatica*, on the basis of the spacing of the posterior eyes. Only three specimens are available. In these the distance from PME to PLE is, respectively, 1.125, 1.667, and 1.882 times the diameter of a PME. This is a little more than the range of variation in *A. bicolor* (80 specimens). In other respects the specimens are quite similar. Recalling the variation of eye spacing shown by *A. philosopha* (=*A. bicolor*) in the same geographic region, it seems best to unite *A. scholastica* and *A. pragmatica* also.

The treatment of all of Chamberlin's species from the islands and shores of the Gulf of California has been difficult. The type localities are difficult of access, only a handful of specimens (some of which have been dried) are in collections, and the extreme climatic conditions of the region are seemingly operating on the animals to produce variation not usual in the genus. The presence of any *Ariadna* at all in such a hot arid region as coastal Sonora is surprising. More specimens are needed, but they may be difficult to find.

Color. Carapace and chelicerae orange-brown. Anterior legs yellow-brown, darker distally. Succeeding legs lightening to yellow. Sternum, endites, and labium yellow-brown to orange-brown, coxae yellow-brown to yellow. Abdomen purplish gray above, yellowish beneath.

Structure. Dimensions of three females: Total length 8.6–12.3 mm, mean 10.33 mm; carapace length 3.9–4.6 mm, mean 4.31 mm; carapace width 2.2–4.1 mm, mean 3.03 mm; sternum length 2.2–4.0 mm, mean 2.94 mm, sternum width 1.33–2.57 mm, mean 1.823 mm.

Investiture. Generally normal. The fringe on anterior legs is less conspicuous than usual.

Spination. See Table 18.

Diagnosis. Only the female is known. The absence of lateral spines from tibiae I and II, and the presence of only two spines in the metatarsal comb separate *A. scholastica* from the other American species.

Distribution. Shore and islands of the Gulf of California.

Records. MEXICO. SONORA: Tepoca Bay, 25 Apr. 1921, ♀, (J. C. Chamberlin), holotype of *A. pragmatica.* GULF OF CALIFORNIA: Patos Island, 23 Apr. 1921, ♀, (J. C. Chamberlin), type of *A. scholastica;* Cedros Island, 22 Feb. 1945, ♀, (B. F. Osorio Tafall).

Ariadna weaveri sp. n.
Figures 50, 53, 56. Map 1.

Holotype. A male from Mexico, Islas Revilla Gigedo, Clarion Island, in American Museum of Natural History. The species is named after my good friend and former professor, Dr. Andrew A. Weaver, who first introduced me to the study of spiders.

Discussion. The sexual dimorphism in this species is much greater than is usual in *Ariadna*. The total body length of the males is only equal to or slightly more than the carapace length of some of the females. The male coloration is lighter than usual in relation to that of the females.

Color. Male. Carapace orange-brown, narrowly flanged marginally, producing a thin dark marginal line in dorsal view. First legs slightly brownish yellow, remaining legs yellow to yellowish white. Chelicerae yellow, endites and labium yellowish white. Sternum yellow suffused with purplish gray. Abdomen yellow suffused with purplish gray laterally and on the lateral parts of dorsum and venter. Dorsum with a broad median band of purplish gray finely mottled with yellowish, the band broadening posteriorly to the full width of the abdomen. Venter with a broad median band of clear yellowish white, the band narrowing posteriorly. Fine transverse yellowish lines break the dorsal band of the abdomen into sections that probably correspond with the (otherwise externally suppressed) segmentation of the abdomen. Seven of these sections are visible in the posterior third of the abdomen anterior to the anal tubercle.

Female. Carapace, chelicerae, palps, and first legs distal to femur mahogany. The first femur and the remaining legs yellow to yellow-brown. Sternum, labium, and endites light mahogany. Abdomen uniform purplish gray above and below in some specimens, yellowish beneath in others.

Structure. Dimensions of two males: Total length 4.0, 5.2 mm; carapace length 1.8, 2.1 mm; carapace width 1.3, 1.6 mm; sternum length 1.3, 1.5 mm; sternum width 0.78, 0.87 mm.

Dimensions of seven females: Total length 7.8–12.2 mm, mean 10.10 mm; carapace length 3.5–6.0 mm, mean 4.68 mm; carapace width 2.2–3.7 mm, mean 2.91 mm; sternum length 2.5–3.5 mm, mean 2.92 mm; sternum width 1.21–1.96 mm, mean 1.541 mm.

Male palp. Bulb small, its greatest diameter about equal to diameter of tibia plus tarsus, and its transverse diameter about twice the width of tibia. Midpiece very short, conical, passing into the embolic portion at a curve. Embolic portion shorter than palpal tibia and not much longer than midpiece. Another shallow bend at tip of embolus. Palpal tibia thickened somewhat at base, but not inflated.

Male first leg. Metatarsus and tarsus slender, almost straight, and entirely without spines or apophyses.

Investiture. Male. Hair very short and sparse on the carapace, tending to be arranged in rather regular longitudinal rows on the cephalic region. Elsewhere arranged as in *A. isthmica*, but lacking the scopulae of hooked hairs on tarsi and metatarsi.

Female. Hair longer and denser than in male, especially on palps and legs.

Spination. See Table 23.

Diagnosis. Male. Metatarsus I nearly straight, slender, without spines or apophyses. Metatarsal comb of three spines. Length of embolic portion of palp less than width of palpal bulb.

Female. Tibiae I and II without lateral spines; ventral spines of tibia II usually 4–2 (the outer row, however, often contains one or two additional spines); metatarsal comb of three spines; usually with 1–2 prolateral spines on tibia III. Carapace length 3.5–6.0 mm, mean 4.68 mm.

Distribution. Mexico, the Revilla Gigedo Islands.

Records. MEXICO. Clarion Island 7–8 May 1955, ♂♂♀♀oo, from log, (McDonald

and Blodget); Socorro Island, 1–5 May 1955, ♀, (McDonald and Blodget).

Ariadna caerulea Keyserling
Figures 44–45, 49. Map 2.

Ariadne caerulea Keyserling, 1877, Verhandl. der könig. kais. Zool. Bot. Gesell., Wien, 1877:227. Female and juvenile syntypes from Colombia, Bogotá, in British Museum (Natural History), examined.

Ariadna caerulea: Petrunkevitch 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):732.

Discussion. This species appears to be, as does *A. pilifera,* more variable in some characters than is usual. One of the six females had only three spines in the metatarsal comb, rather than four, and another had only two lateral tibial spines. It is possible that more than one species is included here but, since each of the females was collected at a different locality, nothing is known of the range of intrapopulation variation. Until more specimens become available only one, presumably variable, species should be recognized.

Color. Male and female. Carapace, anterior legs, chelicerae, and palps reddish mahogany. Legs with longitudinal lighter stripes. Posterior legs paler. Sternum, endites, and labium orange-brown. Abdomen uniform dark purplish gray above, only a little paler beneath, with a bluish surface sheen.

Structure. Dimensions of one male: total length 3.9 mm; carapace length 2.2 mm; carapace width 1.6 mm; sternum length 1.4 mm; sternum width 0.84 mm.

Dimensions of five females: total length 7.8–11.7 mm, mean 9.44 mm; carapace length 4.1–4.7 mm, mean 4.33 mm; carapace width 2.5–2.9 mm, mean 2.64 mm; sternum length 2.0–2.7 mm, mean 2.31 mm; sternum width 1.28–1.63 mm, mean 1.424 mm.

Investiture. Hair long and reddish, distributed as usual. Fringes especially long on femora and tibiae I and II.

Spination. See Table 7.

Diagnosis. Tibiae I and II with lateral spines; tibia II with 4–(3–4) ventral spines. Metatarsus IV with a comb of four spines and usually no additional ones. Metatarsi II and III unarmed retrolaterally, III usually with a total of 5–9 spines.

Male. Metatarsus of first leg slender and straight, without apophyses or modified spines. Metatarsi I and II each with 2–4 spines. Palpal tibia conspicuously inflated, bulb of palp small, length of embolic portion about equal to width of bulb.

Distribution. Colombia and Ecuador, in mountains (Map 2).

Records. COLOMBIA. CUNDINAMARCA: Bogotá (type locality). MAGDALENA: S side of Sierra Nevada de Santa Marta, 8–11,000 ft (2440–3350 m); NARINO: 20 mi. E of Pasto; TOLIMA: 10 mi. W of Ibague; VALLE: 11 mi. W of Cali; 13 mi. W of Cali.

ECUADOR. AZUAY: Lago Zurucuchu, 11 mi. W of Cuenca; PICHINCHA: 7 mi. S of Cayambe; TUNGURAHUA: Baños.

Ariadna cephalotes Simon
Figure 11. Map 2.

Ariadna cephalotes Simon, 1907, Ann. Soc. Ent. Belg., 51:262. Female and juvenile syntypes from Bolivia, San Mateo, in Muséum National d'Histoire Naturelle, Paris, examined. The female specimen is here designated as the lectotype, and the juvenile as a lectoparatype. Petrunkevitch 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):732.

Ariadna hotchkissi Chamberlin, 1916, Bull. Mus. Comp. Zool., 61(3):216, Pl. 10, fig. 4, 5. Immature holotype from Lucma, Cuzco, Peru, in Museum of Comparative Zoology, Cambridge, examined. Bonnet, 1955, Biblio. Aran., 2(1):732. NEW SYNONYMY.

Discussion. Neither *A. cephalotes* nor *A. hotchkissi* has been reported in the primary literature since the original descriptions were published. No additional specimens are available from near the type localities of either. In 1965, however, Levi collected, at Tarma, Peru, a small series of *Ariadna* that agree well with the lectotype of *A. cephalotes.*

The holotype of *A. hotchkissi* is an im-

Map 2

mature specimen. It has a reduced spination as compared with the lectotype of *cephalotes*, but is quite close to the immature lectoparatype of that species. The differences in spination between the latter two specimens are in the ventral spination of the second tibia and the metatarsal comb. Although these are normally highly diagnostic characters, they do vary enough even in single demes to be of doubtful reliability when comparing singly collected specimens with each other.

It seems better, in view of the usually extensive distributions of species in this genus, and the fact that all the specimens in question are from similar mountainous areas, to synonymize *A. hotchkissi* with *A. cephalotes*. If further collecting should demonstrate the distinctness of *A. hotchkissi*, the Peruvian specimens described below should be retained in *A. cephalotes*.

Color. Female. Carapace dark mahogany, chelicerae darker. Legs yellowish brown, anterior legs and distal segments darker. Distal segments of palp almost as dark as carapace. Metatarsi I and II with distinct dark distal annuli, fainter annuli on tibiae I and II and metatarsi III and IV. Abdomen dark purplish gray.

Male unknown.

Structure. Dimensions of eight females: total length 9.2–11.4 mm, mean 9.78 mm; carapace length 4.4–5.0 mm, mean 4.54 mm; carapace width 2.8–3.4 mm, mean 2.93 mm; sternum length 2.6–3.0 mm, mean 2.64 mm; sternum width 1.43–1.70 mm, mean 1.491 mm.

Investiture. As usual.

Spination. See Table 8.

Diagnosis. Generally lacking lateral spines on all tibiae (occasionally 1 or more retrolateral spines on tibia I), ventral spines 4–4 on tibia I, 4–3 on tibia II; abdomen uniform purplish gray.

Distribution. Bolivia and Peru.

Records. BOLIVIA. San Mateo (female lectotype, juvenile lectoparatype).

PERU. APURIMAC: 37 km S. of Andahuaylas, 6 March 1951, ♀oo (E. S. Ross and A. E. Michelbacher); Cuzco: Lucma, 7000 ft (2130 m), Aug. 1911, Yale Peruvian Expedition (holotype of *A. hotchkissi*); JUNÍN: Tarma, 3100 m (10175 ft), 11–12 Feb. 1965, ♀♀, (H. W. Levi), 14 Feb. 1965, "in ground" ♀♀oo, (H. W. Levi).

Ariadna murphyi (Chamberlin), new combination

Map 3.

Dysdera murphyi Chamberlin, 1920, Brooklyn Mus. Sci. Bull., 3(2):38. Female holotype from Peru, Chinchas Island, in Museum of Comparative Zoology, examined. Bonnet, 1956, Biblio. Aran., 2(2):1631.

Discussion. This is an ordinary member of the genus *Ariadna*, without any morphological characters more than usually suggestive of *Dysdera*. Chamberlin seems, for a brief time, to have considered *Ariadna* similar enough to *Dysdera* to warrant uniting the two genera. Later he described additional species in *Ariadna*. The correct placement of *A. murphyi* has not been made known previously. Only the female and juvenile are known.

Color. Carapace and first legs orange-brown to rich reddish mahogany. The other legs paler. Abdomen light purplish gray to grayish yellow above, scarcely paler beneath.

Structure. Dimensions of seven females: Total length 9.0–12.0 mm, mean 10.61 mm; carapace length 4.5–5.9 mm, mean 5.04 mm; carapace width 2.2–3.2 mm, mean 2.86 mm; sternum length 2.4–3.0 mm, mean 2.73 mm; sternum width 1.06–1.71 mm, mean 1.491 mm.

Investiture. Fringes of hair on anterior legs straight, rather than curling. Lateral spines on tibiae I and II very short, half the tibial diameter or less.

Spination. See table 15.

Diagnosis. The presence of only two spines in the metatarsal comb distinguishes *A. murphyi* from most other species. The ventral tibial spination, 4–4 on tibiae I and II, separates it from the other species with two-spined comb.

Distribution. Recorded only from islands off the coast of Peru (Map 3).

Records. PERU. Chinchas Island, 12 Oct. 1919, ♀♀o, (R. C. Murphy), holotype and paratypes; South Chinchas Island, 23 Feb. 1935, ♀♀oo.

Ariadna peruviana sp. n.

Figures 34–35, 39. Map 3.

Holotype. Male from Lima, Lima, Peru, 1939 (W. K. Weyrauch) in the Museum of

Map 3

Comparative Zoology. The name is an adjective referring to the country of origin of the species.

Color. Male. Carapace mahogany. Chelicerae yellowish brown. First pair of legs yellowish brown, the succeeding pairs lightening to yellow. Sternum, labium, endites, and coxae yellow-orange. Palps yellow. Abdomen yellowish white beneath and laterally, with a sooty median dorsal band about one-third the width of the abdomen anteriorly, widening to the full abdominal width posteriorly. Faint darker markings as in the female.

Female. Carapace, chelicerae, palpal tibia and tarsus, and first legs distal to the femur dark reddish mahogany. Succeeding [illegible] lightening to yellow-brown. Labium and endites mahogany. Sternum, coxae, palpal femur and patella yellow-brown. Abdomen purplish gray above, darker in the axial third. Inconspicuous longitudinal lines resembling short dark brush strokes are visible on the dorsum of well-preserved specimens.

In some alcoholic specimens of both sexes the abdomen is almost white except for the sooty wash down the middle. The condition of these specimens suggests that the effect of preservation is chiefly responsible for their paleness. Both the males are light-colored.

Structure. Dimensions of two males: total length 6.8, 6.8 mm; carapace length 3.5, 3.6 mm; carapace width 2.3, 2.5 mm; sternum length 2.1, 2.3 mm; sternum width 1.1, 1.1 mm.

Dimensions of six females: total length

8.3–11.3 mm, mean 9.72 mm; carapace length 3.7–5.3 mm, mean 4.42 mm; carapace width 2.3–3.4 mm, mean 2.81 mm; sternum length 2.3–3.2 mm, mean 2.72 mm; sternum width 1.2–1.8 mm, mean 1.44 mm.

Male palp. Bulb small, twice width of palpal tibia or less. Midpiece of palp much longer than the embolus and about equal to palpal tibia in length. Embolus making about one quarter of a helical turn.

Male first leg. First metatarsus moderately slender and bearing two lateral protuberances or low apophyses, each of which ends in a short thick spine. The retrolateral protuberance is near the base of the metatarsus, the prolateral one is more distal, but still in the proximal half of the metatarsus. The distal spine in the outer ventral row on tibia I is somewhat shortened and thickened.

Investiture. About as usual in both sexes.

Spination. See Table 2.

Diagnosis. Male. The heavy spines of the first metatarsus, placed in the proximal half of the podomere, and not opposite each other, are distinctive for the male of this species.

Female. Lateral spines present on tibiae I and II. Ventral spines of tibiae I and II 4–4 (the proximal inner spine is generally more slender than the others). Metatarsal comb of three spines.

Distribution. Known only from Peru (Map 3).

Records. PERU. LIMA: La Molina, 250 m; Jan. 1961, 4♀♀ (R. Garcia); Lima, 1939, in house, ♂♂♀♀oo (W. K. Weyrauch); Lima, 9 Jan. 1955, o, (E. I. Schlinger and E. S. Ross). LIBERTAD: Jequetepeque, 15 Feb. 1965, o. (L. Peña).

Ariadna maxima (Nicolet)
Figures 2, 18–19, 21. Map 2.

Dysdera maxima Nicolet, 1849, *in* Gay, Hist. fis. y polit. de Chile, 3:341, pl. 2, fig. 6, 6a-d, ♀. Holotype lost. Keyserling, 1877, Verhandl. der könig. kais. Zool.-Bot. Gesell. Wien, 1877:230.

Dysdera virens Nicolet, 1849, *in* Gay, Hist. fis. polit. Chile, 3:342. Holotype lost. Keyserling, 1877, Verhandl. der könig. kais. Zool.-Bot. Gesell. Wien, 1877:230; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):734.

Dysdera incerta Nicolet, 1849, *in* Gay, Hist. fis. polit. Chile, 3:342. Holotype lost. Keyserling, 1877, Verhandl. der könig. kais. Zool.-Bot. Gesell. Wien, 1877:230; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):734.

Dysdera coarctata Nicolet, 1849, *in* Gay, Hist. fis. polit. Chile, 3:344, pl. 2, fig. 7, 7a-c, ♀. Holotype lost. Simon, 1864, Hist. Nat. Araignées, p. 106; Keyserling, 1877, Verhandl. der könig. kais. Zool.-Bot. Gesell. Wien, 1877:230; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1956, Biblio. Aran., 2(2):1619. NEW SYNONYMY.

Ariadna maxima: Simon, 1896, Actes Soc. Sci. Chili, 6:64; 1897, Actes Soc. Sci. Chili, 6:105, 107:1900, Rev. Chil. Hist. Nat., 4:49; 1902, Ergebn. Hamburger Magal. Sammlr., 6(4):11; 1905, Bull. Soc. Ent. Fr., 1905(4):71. F. P.-Cambridge, 1898, Journ. Linn. Soc. London, 27:17. Porter, 1914, Rev. Chil. Hist. Nat. 21 (6):180; 1917, Actes Soc. Sci., Chili, 25(2): 82. Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131. Berland, 1924, Nat. Hist. Juan Fern., Easter Isl., 3(3):423, 426; 1934, Publ. Soc. Biogeogr., 4:168. Bonnet, 1955, Biblio. Aran., 2(1):734.

Discussion. Four of the five species described by Nicolet were collected in the vicinity of Santiago and evidently were based upon different ages, sexes, and colorations of a single species. No types are available for any of the species. Fortunately hundreds of specimens from Chile are on hand, especially from the region of Santiago, but altogether covering most of the length of the country. All but four of the specimens belong to a single species. The fifth species described by Nicolet, *Dysdera longipes* collected in Valdivia, has also been synonymized with *maxima* (Petrunkevitch, 1911; Bonnet, 1955). Recently, however, Levi collected in Valdivia two male and two female *Ariadna* which appear to belong to two additional species. The name *longipes* is being reserved for one of these. Descriptions are deferred until more material is available.

For some reason *Dysdera coarctata* has not previously been synonymized with *maxima*, and has been listed in later works as a *Dysdera* (Porter, 1917; Bonnet, 1956). Nicolet's illustration is obviously of an *Ariadna*, and there is no more reason to regard *coarctata* as a separate species than there is for any of the other synonyms.

Color. In general like that of *A. bicolor*, but on the average darker. Male. Palps yellow-brown. Chelicerae and legs lighter in color than those of the female, mahogany to yellow-brown. Color otherwise as in the female.

Female. Carapace deep reddish mahogany, sometimes with a tinge of maroon. Chelicerae almost black. Distal palpomeres and first legs reddish mahogany, remaining legs lightening to yellowish-brown. Labium and endites chestnut. Sternum and coxae yellow-brown, the sternum darker marginally. Abdomen light to dark purplish gray above and below. Large egg-filled females are paler than those not in reproductive condition, because of the stretching of the cuticle.

Structure. Dimensions of 15 males: Total length 7.7–10.2 mm, mean 8.78 mm; carapace length 4.1–5.6 mm, mean 4.79 mm; carapace width 2.7–3.8 mm, mean 3.15 mm; sternum length 2.6–3.6 mm, mean 3.01 mm; sternum width 1.30–1.75 mm, mean 1.490 mm.

Dimensions of 76 females: Total length 8.3–16.0 mm, mean 12.70 mm; carapace length 4.2–7.7 mm, mean 5.97 mm; carapace width 2.5–4.4 mm, mean 3.42 mm; sternum length 2.5–4.5 mm, mean 3.46 mm; sternum width 1.30–2.30 mm, mean 1.723 mm.

Male palp. Bulb small, tibia moderately inflated, the width of the bulb equal to or less than tibial width. Midpiece and embolic portion together shorter than tibia. Midpiece not clearly distinguishable from the embolic portion, the latter wider than in other species.

[illegible] first leg. Metatarsus and tarsus straight, the metatarsus without apophyses or modified spines.

Investiture. Hair long, clothing entire body rather densely, in normal pattern. Fringes of anterior legs of female not very conspicuous.

Spination. See Table 12.

Diagnosis. Male. Metatarsus straight and not notably slender, lacking apophyses and modified spines. Metatarsal comb of four spines. Embolic portion and midpiece of palp together less than palpal tibia in length.

Female. Lateral spines present on tibiae I and II, 4–4 ventral spines on tibiae I and II; four spines in metatarsal comb, plus 1–2 other ventral spines on the same podomere; metatarsus III with 5–9 spines, none retrolateral; carapace length 4.2–7.7 mm, mean 5.97 mm.

Distribution. Chile, including Juan Fernandez Islands.

Records. CHILE. ACONCAGUA: San Felipe. ANTOFAGASTA: Tal-tal. CAUTIN: Temuco; Villarica, garden, and on buildings; NE of Villarica; 30 km NE of Villarica. COLCHAGUA: Chepica; Cunaco, Fundo Millahue. CONCEPCIÓN: Concepción; Bosque de Ramuntcho; Talcahuana. COQUIMBO: La Serena; Pichidangui, Isla de los Locos. LINARES: Linares. LLANQUIHUE: 2–3 km NW of Ensenada; Peulla, 200 m, on buildings; Petrohué, buildings; Puerto Varas, 50 m, buildings; Parque Philippi. MAGELLANES: Punta Arenas. NUBLÉ: Chillan, Cordillera de Chillan. OSORNO: Osorno, city park; Purranqme; Termas de Puyehue, 240 m, buildings and gardens. SANTIAGO: Alhué; Cerro Santa Lucia; El Canelo; Quinta Normal; Tiltil; Yeso River, 1200 m, Cordilleras near Santiago. TALCA: Alto de Vilches, Andes; Talca. VALDIVIA: Valdivia, Isla Teja, farmland. VALPARAISO: Bosque Relicto; Lagunillas; Limache; Los Horcones; Quintero, Playa Piratas; Ventana; Viña del Mar.

JUAN FERNANDEZ ISLANDS: *Más a Tierra:* Bahia Cumberland; Galpon, Valle

Villagro; Puerto Ingles; Quebrada Pangal, Monte Oscuro, 100m; *Más Afuera:* Cerro Innocentes, 1000 m; Chorro Dona Anna; Chorro de Varadero; Plano de Chosa, 800–1000 m; Quebrada Casa; Quebrada Vaca.

Ariadna isthmica sp. n.
Figures 23–25, 30. Map 1.

Ariadna comata: Banks, 1929, Bull. Mus. Comp. Zool., 69(3):54. Not *A. comata* O. P.-Cambridge.

Holotype. A male from Panama, Barro Colorado Island, in the Museum of Comparative Zoology. The name is an adjective meaning isthmian, in reference to the species' Central American distribution.

Discussion. There appears to have been no reason, other than a guess based on distribution, for Banks' assignment of this species to *Ariadna comata.* As noted above, *A. comata* is here considered a synonym of *A. pilifera.* The present species is entirely Central American in distribution, while *pilifera* is recorded only from the southwestern United States and Mexico.

Color. Male. Carapace light to dark orange-brown with a narrow dark marginal line. Cephalic region lighter. Eyes narrowly rimmed with black. Chelicerae, labium, endites, and legs yellow to orange-brown, the anterior legs only slightly darker. Sternum yellow with a suffusion of purplish gray. Abdomen purplish gray over yellowish above, the yellowish showing through as many tiny light flecks. Venter of abdomen yellowish white with a dusting of purplish gray. Spinnerets and anal tubercle yellowish white.

Female. Coloration generally as in male, but tending to be darker, the carapace and first legs often a rich reddish mahogany. Legs sometimes suffused with purplish gray at distal ends of podomeres.

Structure. Dimensions of three males: Total length 4.6–6.9 mm, mean 6.00 mm; carapace length 2.4–3.3 mm, mean 2.93 mm; carapace width 1.6–2.2 mm, mean 1.92 mm; sternum length 1.5–2.0 mm, mean 1.78 mm; sternum width 0.92–1.12 mm, mean 1.020 mm.

Dimensions of seven females: Total length 7.5–11.7 mm, mean 9.04 mm; carapace length 3.4–4.2 mm, mean 4.14 mm; carapace width 2.1–2.6 mm, mean 2.28 mm; sternum length 2.0–2.4 mm, mean 2.14 mm; sternum width 1.14–1.35 mm, mean 1.227 mm.

Male palp. The bulb of the palp is small, its diameter less than twice that of the palpal tibia. The midpiece is short and narrows abruptly to the embolic portion, which joins the midpiece at a curve of almost ninety degrees. The embolic portion is equal to or slightly longer than the palpal tibia, and makes another nearly ninety degree bend at the tip. The palpal tibia is somewhat thickened at the base, but not inflated.

Male first leg. Metatarsus and tarsus slender and sinuous, without thickened spines or apophyses.

Investiture. Male. Entire body with a sparse coating of fairly long dark, curving hair, most of it making about a 45 degree angle with the cuticular surface. A few scattered hairs are straight, stiff, and almost erect. The chelicerae, tips of the endites, and tarsus of the palp are more densely clothed with hair than the rest of the body. On all the legs, most conspicuously the fourth, the tarsi and distal part of the metatarsi bear scopulae of stiff, short, translucent bristles bent into a minute hook at the tip.

Female. Differing from the male only slightly. Hair denser on metatarsi and tibiae of the first two legs, usually forming a conspicuous fringe. The scopular hairs of the male are replaced by long curved recumbent hairs without hooked tips.

Spination. See Table 11.

Diagnosis. Male. First metatarsus slender and sinuous, without apophyses or modified spines. Embolic portion of palp equal to palpal tibia in length or slightly longer. Metatarsal comb of four spines. Carapace length 2.4–3.3 mm. First tibia

usually with 3–5 retrolateral spines. Legs not annulate.

Female. Lateral spines present on tibiae I and II. Ventral tibial spines 4–4 on legs I and II. Metatarsal comb of four spines. Metatarsi II and III unarmed retrolaterally. A spine on palpal patella. Tibia III usually with one to two prolateral spines. Metatarsus III with seven to eight spines.

Distribution. Central America (Map 1).

Records. NICARAGUA. Musawas: Huaspuc River.

PANAMA. Bella Vista; Porto Bello. CANAL ZONE: Barro Colorado Island; Fort Sherman; Canal Zone Forest Preserve; Canal Zone Biological Area; Fort Davis; Gamboa.

Ariadna tovarensis Simon
Map 4.

Ariadne tovarensis Simon, 1893, Ann. Soc. Ent. Fr., 61:448. Female and immature syntypes from Venezuela, Colonia Tovar, in Muséum National d'Histoire Naturelle, Paris, examined.
Ariadna tovarensis: Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):738.

Discussion. As is the case with several other South American species, *A. tovarensis* is known from only a few specimens, so that variability of the diagnostic characters is poorly known. The geographically nearest species, *A. tubicola*, *A. caerulea*, and *A. solitaria*, are, however, distinguished by characters that seem to warrant recognition of *tovarensis* as a distinct species.

Color. Carapace light mahogany, paler in cephalic area. Legs unmarked yellow to brownish yellow, the first leg a little darker than the others. Chelicerae, endites, labium and sternum brownish yellow. Abdomen shrunken from cuticle, but apparently was unmarked purplish gray above, scarcely lighter beneath.

Structure. Dimensions of two females: Total length 7.3, 7.4 mm; carapace length 2.7, 3.1 mm; carapace width 2.1, 2.2 mm; sternum length 1.6, 2.0 mm; sternum width 0.98, 1.14 mm.

Investiture. Much of the hair has been rubbed off. The pattern seems to be normal, the density perhaps a little less than usual. Fringes on the anterior legs are straight or slightly curved.

Spination. See Table 21.

Diagnosis. Lateral spines present on tibiae I and II; ventral tibial spines 4–4 on leg I, 4–3 on leg II, with proximal inner spine reduced on tibia II; metatarsal comb of four spines, no other ventral spines on fourth metatarsus; metatarsi II and III unarmed retrolaterally.

Distribution. Known only from north central Venezuela.

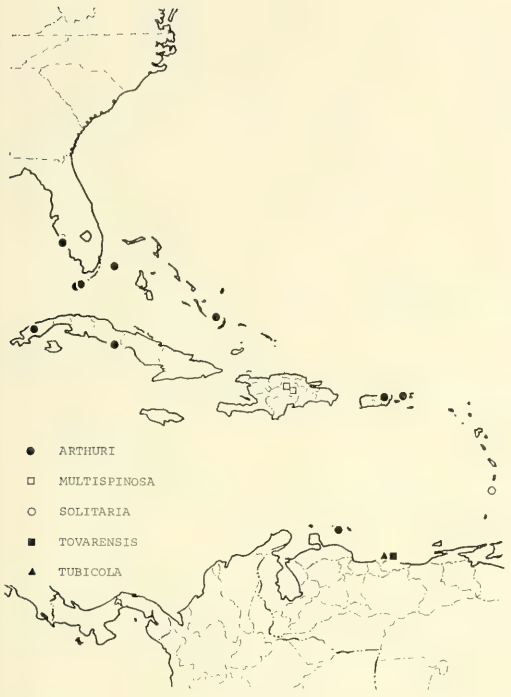
Records. VENEZUELA. DISTRITO FEDERAL: Colonia Tovar, ♀♀o, (E. Simon), the syntypes; La Silla, NE of Caracas, 21 Dec. 1930, ♀, (J. G. Myers).

Ariadna arthuri Petrunkevitch
Figures 8, 26–27, 32. Map 4.

Ariadna arthuri Petrunkevitch, 1926, Trans. Connecticut Acad. Arts Sci., 28:48, fig. 8–10, "♀". Immature holotype from Sta. Maria Bay, St. Thomas, Virgin Islands, in Peabody Museum, Yale, New Haven, not seen; *ibid.*, 1929, Trans. Connecticut Acad. Arts Sci., 30:59, figure 41, o.
Ariadna bicolor: Lutz, 1915, Ann. New York Acad. Sci., 26:81; Franganillo, 1936, Los Arácnidos de Cuba hasta 1936, p. 38. Not *A. bicolor* (Hentz).
Ariadna solitaria: Lutz, 1915, Ann. New York Acad. Sci., 26:81. Not *A. solitaria* Simon.

Discussion. The holotype of *A. arthuri* could not be located by Petrunkevitch when an attempt was made to borrow it in 1962. Types of both the other West Indian species have been examined and are distinctly different. The name *A. arthuri* is here applied to the common wide-ranging species found from southern Florida to Curaçao—almost certainly the one to which it belongs.

Petrunkevitch (1929) described and illustrated a second immature specimen of *A. arthuri*, collected on Desecheo Island, 18–20 February 1914. Presumably this spider is the one collected by Lutz and mentioned by him in his list of Greater Antillean spiders (1915) as *A. solitaria*. I have



Map 4

examined the specimen and find that, while Petrunkevitch's description is wrong in many details, the identification as *A. arthuri* is correct.

The specimen, or specimens, from Cuba, listed by Lutz (1915) as *A. bicolor*, have not been seen. All available material from Cuba belongs to *A. arthuri*, however. Franganillo (1936) simply cites *A. bicolor* as occurring in Cuba with no further data. Probably his citation is based upon Lutz's paper, to which he refers.

Color. Male and female. Carapace, sternum, and all appendages yellow to orange, slightly darker on first legs, chelicerae, and palpal tarsus (palps entirely light in male). Abdomen dusky yellow beneath and on sides, purplish gray above and around spinnerets ventrally.

Structure. Dimensions of two males: total length 4.0, 4.5 mm; carapace length 2.1, 2.2 mm; carapace width 1.4, 1.5 mm; sternum length 1.36, 1.44 mm; sternum width 0.82, 0.82 mm.

Dimensions of four females and two last instar juveniles: total length 4.8–7.0 mm, mean 5.98 mm; carapace length 2.0–3.5 mm, mean 2.67 mm; carapace width 1.2–2.2 mm, mean 1.64 mm; sternum length 1.2–2.1 mm, mean 1.55 mm, sternum width 0.73–1.14 mm, mean 0.922 mm.

Male palp. The bulb is quite small and the tibia moderately inflated, the diameter of the bulb equalling 1.5 times the tibial diameter or less. The midpiece of the bulb is longer than either the spine or the depth of the bulb, and equals or slightly exceeds the length of the tibia.

Male first leg. The tarsus and metatarsus are sinuous and slender. The middle third of the metatarsus is swollen. The inflation of the podomere is greatest at two-thirds of the distance from base to tip of the metatarsus. At this point, and opposite each other, are two ventrolateral protuberances; these are greatly enlarged spine sockets, each bearing a short thick spine. The distal pair of metatarsal spines and their sockets are somewhat enlarged also. The distal spine of the retrolateral ventral row on the tibia is slightly enlarged and flattened.

Investiture. Male. Spines are conspicuous, mostly stout, and of medium length. On the first tibiae the longest spines equal or slightly exceed the tibial diameter. Hair mostly as usual. The tarsi of all legs except the first pair bear ventral scopulae.

Female. Metatarsal and tibial spines on legs I and II lie at a very small angle to the podomeres, and the tips of the longer ones tend to curve inward toward the long axis of the leg. All the spines are slender, and the primary ones are very long, equalling or considerably exceeding half the length of the podomere.

Spination. See Table 3.

Diagnosis. Female. The presence of more than 4–4 ventral spines on tibiae I and II, and two spines in the metatarsal comb distinguish *A. arthuri* from all other American species except *A. tarsalis*. The latter may be separated by its

larger size, the lateral spination of the first two tibiae (see key or table), and distribution.

Male. The structure of the first leg distinguishes this species from the other known males. Specific diagnostic characters are the heavy spines set opposite each other distal to the middle of the metatarsus.

Distribution. Southern Florida and islands of the Gulf of Mexico and Caribbean (Map 4).

Records. FLORIDA: *Lee Co.,* Boca Grande, under rocks. *Monroe Co.:* Big Pine Key, some taken from cracks and shipworm burrows in driftwood on beach; Bill Find's Key, under bark of red mangrove; Rattlesnake Key, under bark of red mangrove; Squirrel Key, under bark of red mangrove.

WEST INDIES. BAHAMA ISLANDS: *South Bimini; Crooked Island.* CUBA: 7 km N of Viñales, Trinidad Mtns., Buenos Aires; Soledad. CURAÇAO: Siberië, 3 km N of Savonet, "stones"; Piscadera Bay. PUERTO RICO: Aguas Buenas, "cave entrance"; Desecheo Island, "under fallen leaves in a sea-grape thicket." VIRGIN ISLANDS: St. Thomas, Santa Maria Bay, "under bark of a log," the holotype. LESSER ANTILLES: no further data.

Ariadna multispinosa Bryant
Map 4.

Ariadna multispinosa Bryant, 1948, Bull. Mus. Comp. Zool., 100(4):339. Female holotype from Dominican Republic, Loma Rucilla Mtns, in Museum of Comparative Zoology, examined.

Discussion. Although known only from one female and one juvenile, *A. multispinosa* is quite distinct from most other species. Five species are similar to *multispinosa* in some characters of the spination, but are distinguished by other characters that have high diagnostic value. Only *A. arthuri* and *A. tarsalis* are very close to *multispinosa* in structure. Until mature males and female of the latter two species are available, the relationships cannot be adequately assessed.

Color. Carapace brown, legs yellowish brown, abdomen dark purplish gray above, dirty yellowish beneath.

Structure. Dimensions of female holotype: Total length 9.4 mm; carapace length 4.1 mm; carapace width 2.6 mm; sternum length 2.0 mm; sternum width 1.33 mm.

Investiture. Normal.

Spination. See Table 14.

Diagnosis. The absence of lateral spines from tibiae I and II, and presence of eight to eleven ventral spines in each row on tibiae I and II separate *A. multispinosa* from all other described American species.

Distribution. Known only from Hispaniola.

Records. DOMINICAN REPUBLIC. Loma Rucilla Mtns, Pico del Yaque, 8–19,000 ft (2440–3050 m), June 1938, ♀, (P. J. Darlington, Jr.), holotype; Cordillera Central, near Valle Nuevo, rain forest, 6000 ft (1830 m), Aug. 1938, o, (P. J. Darlington, Jr.), Paratype.

Ariadna tarsalis Banks
Map 3.

Ariadne tarsalis Banks, 1902, Proc. Washington Acad. Sci., 4:57, plate 1, figure 9, immature. Immature holotype from Culpepper I., Galapagos Islands, in Museum of Comparative Zoology, Cambridge, examined. Banks, 1924. Zoologica, 5(9):95.

Ariadna tarsalis: Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):737.

Discussion. This species is quite similar to *A. arthuri* Petr. of the West Indies. Unfortunately adequate comparison of the two species is impossible, because *A. tarsalis* is known only from six immature specimens. The spination character that separates the two species is a minor one, but the difference in size is considerable.

Color. Carapace and first legs orange-brown, the remaining legs paler orange to yellow-orange. Sternum and coxae yellow-orange, endites and labium brownish.

Abdomen purplish gray above, paler beneath.

Structure. Dimensions of holotype: Total length 7.5 mm, carapace length 3.7 mm, carapace width 2.3 mm, sternum length 2.1 mm, sternum width 1.08 mm.

Investiture. Normal.

Spination. See Table 20.

Diagnosis. Lateral spines usually present on tibiae I and II, ventral spines on these tibiae usually 6–6 or more; metatarsal comb of two spines; tibia I with 1–2 retrolateral spines, tibia II with none; carapace length 3.7–4.8 mm, mean of three specimens 4.15 mm.

Distribution. The Galapagos Islands.

Records. GALAPAGOS ISLANDS: *Culpepper Island,* immature holotype. *South Seymour Island,* April 1923, o, (N. Banks). *Duncan Island,* 23 June 1929, oo, (H. H. Cleaves). *Indefatigable Island,* 20 June 1929, oo, (H. H. Cleaves).

Ariadna mollis (Holmberg)
Figures 1, 16, 17, 22. Map 2.

Segestria mollis Holmberg, 1876, An. Agric. de la Repub. Argentina, 4:25, figure 6, ♀. Holotype from Buenos Aires (?), lost.

Segestria vulgarissima Holmberg, 1876, *ibid.,* 4: 25, figure 7, ♀. Holotype from Buenos Aires, lost.

Ariadna mollis: Mello-Leitão, 1933, Arch. Escol. Sup. Agric. Med. Vet., 10(1):12; 1944, Rev. Museo La Plata, 3(24):312, 322, figure 1, ♂; 1947, Arq. Museu Paranaense, 6(6):233, 234. Bonnet, 1955, Biblio. Aran., 2(1):735.

Discussion. After examining specimens from Buenos Aires and Montevideo, Mello-Leitão (1933) concluded that only one *Ariadna* with a dorsal abdominal pattern occurred in these regions. Consequently he synonymized *S. vulgarissima* and *A. boesenbergii* with *S. mollis,* at the same time correctly transferring *mollis* to the genus *Ariadna.*

Because the paper is likely to be inaccessible to many people, I here quote Mello-Leitão's discussion in full: "Tendo examinado exemplares de *Ariadna* da Provincia de Buenos Aires e de Montevideo (colhidos por mim no Cerro) e confrontando-os com as descricões de Holmberg e de Keyserling, conclui pela identidade das mesmas, tendo prioridade a designacão de Holmberg." Working only from descriptions as he apparently was, (that is, without any type specimens), it is not surprising that Mello-Leitão came to this conclusion. Keyserling's description is reasonably detailed, but those of Holmberg are almost devoid of useful information.

An examination of two specimens from the type series of *A. boesenbergii* (including both sexes) and a series of specimens from Buenos Aires reveals that *mollis* and *boesenbergii* are similar but distinct and apparently partly sympatric species. One vial from the Museo Argentino de Ciencias Naturales contained two female *mollis* and two female *boesenbergii.* The two species are almost identical in appearance, but are distinguished by several features of the spination.

The ecological relationships of *mollis* and *boesenbergii* should be carefully investigated. Not only are they different from most *Ariadna* in having an abdominal pattern, but they appear also to be sympatric sibling species that would be of interest as a study of character displacement or its absence. At present there are too few specimens available from too limited an area to suggest whether or not character displacement has occurred.

Mello-Leitão, in several papers, (1940, 1941, 1944, 1945, 1946), has given distribution records for *A. mollis* and *A. boesenbergii* that include many localities not listed below. His identifications of neither species are trustworthy, so the actual distribution of both species remains uncertain.

Color. Male. Carapace and chelicerae orange-brown. First legs a little lighter than carapace, the remaining legs progressively paler posteriorly. Sternum the color of the femora. Abdomen yellowish white dorsally with a purplish gray median longitudinal band in the anterior half and a series of short transverse bars posteriorly.

Female. Essentially as in male. The carapace and legs are darker, a rich reddish mahogany. The abdominal pattern on a female with enlarged abdomen consists of a lozenge anteriorly, back of which is a series of forward pointing chevrons. A narrow median band connects the first chevron to the lozenge, and continues to the anterior end of the abdomen (Fig. 1). The sides and venter of the abdomen are purplish gray.

Structure. Dimensions of one male: Total length 7.1 mm, carapace length 3.6 mm, carapace width 2.3 mm, sternum length 2.2 mm, sternum width 1.22 mm.

Dimensions of nine females: Total length 9.9–13.4 mm, mean 11.10 mm; carapace length 4.4–5.4 mm, mean 4.84 mm; carapace width 2.4–3.2 mm, mean 2.79 mm; sternum length 2.4–3.1 mm, mean 2.75 mm; sternum width 1.43–2.00 mm, mean 1.573 mm.

Male palp. Bulb small, only slightly wider than tibia. Tibia scarcely inflated. Midpiece and embolic portion of palp equal to each other in length or midpiece a little shorter.

Male first leg. Metatarsus and tarsus slender, sinuous, lacking apophyses or modified spines. Patella with a prolateral spine.

Investiture. Male generally without unusual features. Tarsi of legs II–IV scopulate ventrally. Female as usual.

Spination. See Table 13.

Diagnosis. Male. First metatarsus sinuous, lacking apophyses and modified spines, metatarsal comb of five to seven spines; midpiece of palp short, about equal to embolic portion in length, abdomen with dorsal pattern.

Female. Separated from most other American *Ariadna* by the pattern of bars on the abdominal dorsum. Presence of lateral spines on tibiae I and II, 4–3 ventral spines on tibia II, and 5–7 spines in the metatarsal comb distinguish it from *A. boesenbergii.* Two other South American species reported to have abdominal patterns, *A. conspersa* and *A. crassipalpus,* are not well enough known to be distinguished from *A. mollis.* (See discussion of these species under *Ariadna* Incertae Sedis below.)

Distribution. Argentina and southern Brazil.

Records. BRAZIL. PARANÁ: Caviana I., 1947, ♀, (A. Maller).

ARGENTINA. BUENOS AIRES: San Isidro, Oct. 1963, ♀; Punta Lara, 6 Apr. 1950, ♀♀oo; Moreno, Oct. 1947, ♀♀, (R. D. Schiapelli); Tigre, Nov. 1940, ♂, (F. Monros); Gral. Madariaga, Jan. 1962, ♀♀, (M. E. Galiano).

Ariadna boesenbergii Keyserling
Figures 3, 46–48. Map 2.

Ariadne Bösenbergii Keyserling, 1877, Verhandl. der könig. kais. Zool.-Bot. Gesell., Wien, 1877: 223, pl. 7, fig. 7, 7a-b, ♂. Syntypes from Montevideo, Uruguay, in the Zoologisches Staats-Museum, Hamburg, examined.

Ariadna bösenbergi: Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:130.

Ariadne bösenbergi: Gerhardt, 1921, Arch. Natur., 87:92, 93, fig. 6, ♂.

Ariadna mollis: Mello-Leitão, 1933, Arch. Escol. super. agricul. med. vet., 10(1):12 (in part); *ibid.,* 1947, Arq. Mus. Paranaense, 6:234. Bonnet, 1955, Bibliog. Aran., 2(1):730, 735. Not *A. mollis* (Holmberg).

Discussion. Mello-Leitão (1933) mistakenly synonymized *A. boesenbergii* with *A. mollis,* and later (1947) reiterated the synonymy in statements prefacing a key to Brazilian *Ariadna.* The two species are similar in size and appearance, but details of spination clearly separate them. Bonnet (1955) followed Mello-Leitão's treatment, at that time the most recent taxonomic opinion.

Among material borrowed from the Museo Argentino de Ciencias Naturales, I found a vial containing four female *Ariadna* collected at Moreno, Buenos Aires. Two of these specimens were *A. mollis,* the other two *A. boesenbergii.* The circumstances of occurrence of the spiders are unknown, but certainly at least a strong

presumption of sympatry is warranted. Only one other instance of collection of two species of *Ariadna* at one locality is known to me. (See under *A. boliviana*).

Coloration. In both sexes the coloration is very similar to that of *A. mollis*, orange-brown carapace and legs, dorsum of abdomen yellow with purplish gray transverse bars.

Structure. Dimensions of male lectotype: total length 8.0 mm; carapace length 3.7 mm; carapace width 2.4 mm; sternum length 2.1 mm; sternum width 1.1 mm.

Dimensions of three females: total length 7.9–9.5 mm, mean 8.63 mm; carapace length 3.6–4.2 mm, mean 3.78 mm; carapace width 2.1–2.4 mm, mean 2.21 mm; sternum length 2.0–2.4 mm, mean 2.12 mm; sternum width 1.1–1.2 mm, mean 1.12 mm.

Male palp. The bulb is small, the tibia short and much inflated, the diameter of the bulb equals less than 1.5 the tibial diameter. The mid-piece of the bulb is longer than either the depth of the bulb or the embolic portion, and slightly exceeds the length of the tibia.

Male first leg. The metatarsus and tarsus are slender and slightly curved, but not sinuous. No apophyses, protuberances, or unusually heavy spines are present on the metatarsus.

Investiture. Hair pattern presenting no unusual features.

Spination. See Table 5.

Diagnosis. Female. No prolateral or retrolateral spines on tibiae I or II; 4–4 ventral spines on tibiae I and II; dorsum of abdomen with a pattern of transverse bars on contrastingly colored background.

Male. First metatarsus slender, not or only very slightly sinuous, without apophyses or heavy spines. Metatarsal comb of 4 spines. Embolic spine shorter than palpal tibia, the latter short and inflated. Abdomen with dorsal pattern as in female.

Distribution. Southern Brazil, Uruguay, east central Argentina (Map 2).

Records. BRAZIL. RIO GRANDE DO SUL: Rio Grande.

URUGUAY. MONTEVIDEO (♂ and ♀ syntypes).

ARGENTINA. BUENOS AIRES: Moreno, Oct. 1947, ♀♀ (R. D. Schiapelli).

Ariadna boliviana Simon
Figures 4, 6, 14, 51–52, 54–55.
Map 3.

Ariadna boliviana Simon, 1907, Ann. Soc. Ent. Belg., 51:262. Male and female syntypes from Espíritu Santo, Bolivia, in Muséum National d'Histoire Naturelle, Paris, examined. Petrunkevitch, 1911, Bull. Am. Mus. Nat. Hist., 29:130.

Discussion. The odd distribution pattern of the two known collections of this species is probably a result of lack of thorough coverage of the area by collectors. Both collections are from upland areas, but a wide lowland, the Gran Chaco, lies between them. In comparing males from the two localities, I can find no significant difference between them. Since other species of the genus have a rather large elevational range (p. 442) it is probable that *A. boliviana* occurs in suitable habitats in the Gran Chaco.

Color. Female. Carapace light orange-brown, darker in cephalic region. Legs yellow-brown, anterior legs and distal podomeres darker. Faint darker distal annuli on tibiae and metatarsi I and II. Abdomen pale purplish gray above, yellow on sides and venter.

Male. Carapace uniform mahogany, with very faint streaks radiating from thoracic groove. Abdomen purplish gray above, dirty yellow beneath. Legs yellow brown, first pair darker. Conspicuous purplish gray distal annuli on first tibia and metatarsus, fainter annuli on second tibia and metatarsus.

Structure. Dimensions of two males: total length 6.5, 6.5 mm; carapace length 3.2, 3.4 mm; carapace width 2.1, 2.2 mm; sternum length 1.6, 2.0 mm; sternum width 1.10, 1.08 mm.

Dimensions of a single female: total length 7.8 mm; carapace length 3.8 mm; carapace width 2.4 mm; sternum length 2.3 mm; sternum width 1.37 mm.

Male palp. Bulb of medium size, tibia somewhat inflated. Diameter of bulb more than 1.5 times that of tibia. Midpiece of palp short, less than diameter of bulb, about half the length of embolic portion. Embolic portion equalling tibia in length.

Male first leg. Metatarsus and tarsus slender and sinuous, without apophyses or heavy spines. Tibia with ordinary spines only, none modified.

Investiture. Male. Hair short and very sparse on carapace, otherwise normal. Tarsi and distal portion of metatarsi II–IV with ventral scopulae of short, translucent, minutely hooked bristles. Spines of relatively short to medium length, those on tibiae I and II shorter than, to slightly longer than, diameter of podomere.

Female. Normal.

Spination. See Table 6.

Diagnosis. Male. Metatarsus I slender and sinuous, lacking apophyses and modified spines; bulb of palp small, embolic portion about equal to palpal tibia in length; metatarsal comb of four spines; metatarsi and tibiae I and II with purplish gray distal annuli; carapace length 3.2–3.4 mm.

Female. Lateral spines present on tibiae I and II; 4–4 ventral spines on tibia I, 4–(2–3) on tibia II; metatarsal comb of four spines; metatarsi III bearing 9–12 spines of which 1–2 are retrolateral.

Distribution. Bolivia, southeastern Brazil (Map 3).

Records. BOLIVIA. ESPIRITU SANTO. ♂ and ♀ syntypes. (Garlepp).

BRAZIL. MINAS GERAIS: Diamantina, Minas de Serrinha, ♂, 1945 (Eliz. Cohn).

Ariadna fidicina (Chamberlin), new combination

Figure 10. Map 1.

Citharoceps fidicina Chamberlin, 1924, Proc. California Acad. Sci., (4)12(28):608. Immature holotype from Ensenada, Baja California del Norte, in California Academy of Science, examined.

Citharoceps californica Chamberlin and Ivie, 1935, Bull. Univ. Utah, 26(4):8, Figs. 22–23, ♀. Female (?) holotype from Laguna Beach, California, in University of Utah collection, not seen. NEW SYNONYMY.

Discussion. In its pattern of spination *A. fidicina* is rather divergent from most other *Ariadna*, but no more so than a few other undoubted *Ariadna* (e.g. *A. gracilis*). The genus *Citharoceps* was erected on the basis of the remarkable large coarse stridulating patches on the carapace. In the absence of males, the synonymy of *Citharoceps* with *Ariadna* may seem doubtful. The female, however, is clearly an *Ariadna* that happens to have stridulating grooves. Discovery of the male is expected to confirm the synonymy.

The holotype of *C. fidicina* was listed (Chamberlin, 1924) as being a female. The specimen has been dried, and is in very poor condition at present. It appears to be immature.

Citharoceps californica was described (Chamberlin and Ivie, 1935) in part as follows: "A larger and darker species than *C. fidicina* Chamberlin, which it otherwise resembles very closely. Known only from immature specimens, which range up to 9 mm in length." The holotype of *C. californica* was not available, but I have examined four of the paratypes (same collection data as the holotype) and find they are all mature. The size and color differences between the two described species are as one would expect as a consequence of the age difference.

Several appendages are missing from the holotype of *C. fidicina*, so that comparison of spination is scarcely possible. A paratype, from the collection of the Museum of Comparative Zoology, was also examined. There is no significant difference in any character between paratypes of *C. fidicina* and *C. californica* of similar size. There can be scarcely any question that the two are synonymous.

Color. Carapace a dark mahogany. Chelicerae and palps darker than carapace, legs lighter than carapace. Anterior legs darkest, the others progressively lighter posteriorly. Sternum orange-brown. Abdomen dark purplish gray above, sometimes with a series of yellow transverse markings producing an indistinctly barred pattern. Venter dirty yellowish mottled with purplish gray.

Structure. Dimensions of ten females: Total length 7.8–10.8 mm, mean 8.97 mm; carapace length 3.6–4.5 mm, mean 4.00 mm; carapace width 2.1–2.7 mm, mean 2.35 mm; sternum length 2.0–2.4 mm, mean 2.23 mm; sternum width 1.16–1.43 mm, mean 1.302 mm.

Investiture. Perhaps a little more densely clothed with hairs ventrally than other species, but the difference is scarcely noticeable in most preserved specimens. The spines are proportionately shorter than usual. The tibial spines are shorter than the diameter of the tibiae, and even the primary spines of metatarsi I and II exceed the metatarsal diameter only slightly. The extra pair of apical ventral spines on the metatarsi are usually between the distal spines of the two ventral rows.

Spination. See Table 9.

Diagnosis. The presence of a patch of coarse stridulating grooves on each side of the cephalic region immediately distinguishes *A. fidicina* from all other American *Ariadna.* In addition, the first and second metatarsi have four apical ventral spines, also a unique character among the American species. The metatarsal comb contains five to six spines.

Distribution. Pacific Coastal region of North America from Pacific Grove, California, to Ensenada, Baja California.

Records. CALIFORNIA. *Monterey Co.:* Pacific Grove; *Los Angeles Co.:* Glendale, Santa Monica Mtns, Saddle Peak, Agoura; *Orange Co.:* Laguna Beach, under bark of trees, holotype and paratypes of *Citharoceps californica;* Santa Ana Canyon, 12 mi. E of San Juan Capistrano.

MEXICO. BAJA CALIFORNIA DEL NORTE: Ensenada, holotype and paratypes of *Citharoceps fidicina.*

Ariadna gracilis Vellard
Figures 7, 28–29, 33. Map 2.

Ariadna gracilis Vellard, 1924, Arch. Inst. Vital Brazil, 2(2):160, figure 45, ♂. Male holotype from Caxias, Maranhão, originally deposited in collection of the Instituto Vital Brazil, not seen. Bonnet: 1955, Biblio. Aran., 2(1):732.

Discussion. According to a letter from Dr. Roched A. Seba of the Institute, the holotype of *A. gracilis* is no longer in the collection of the Instituto Vital Brazil. Fortunately Vellard's paper contains one of the few adequate descriptions of an *Ariadna* species, and a male in the collection of the Museum of Comparative Zoology matches the description closely. Assignment to this species of the females described below is based in part upon similarities in size, coloration, and metatarsal comb. The distribution of the female specimens, all unquestionably belonging to a single species, suggests further that *A. gracilis* is the common, if not the only, *Ariadna* throughout the Amazon Basin.

Ariadna obscura Blackwall and *A. taperae* Mello-Leitão are described as having a single apophysis on the first metatarsus of the male, at least similar to that of *A. gracilis.* Either or both of these could conceivably be synonymous with *gracilis,* but their occurrence outside the Amazon Basin suggests otherwise. Mello-Leitão himself (1947) later synonymized *A. taperae* and another of his own species, *A. campinensis,* with *obscura,* without giving reasons for doing so. No decisive information can be derived from the descriptions of any of these three species.

Color. Carapace rich reddish brown to duller mahogany brown. The appendages and underside of cephalothorax show the usual pattern of variation with respect to carapace color. Abdomen purplish gray above and yellowish to entirely yellowish white beneath. Anterior legs of male

darker than those of female, otherwise the sexes are similar in coloration.

Structure. Dimensions of one male: Total length 5.9 mm; carapace length 3.1 mm; carapace width 2.0 mm; sternum length 2.0 mm; sternum width 1.06 mm.

Dimensions of thirteen females: Total length 7.1–9.8 mm, mean 8.59 mm; carapace length 3.7–4.6 mm, mean 4.14 mm; carapace width 2.2–2.9 mm, mean 2.4 mm; sternum length 2.2–2.9 mm, mean 2.49 mm; sternum width 1.16–1.63 mm, mean 1.347 mm.

Male palp. Bulb very small, in retrolateral view its diameter not exceeding the maximum diameter of the tibia. Tibia somewhat inflated; midpiece of palp longer than spine or embolic portion, shorter than tibia. Midpiece and embolic portion together slightly longer than tibia. An inner distal spine on the tibia.

Male first leg. Metatarsus slender, sinuous, bearing a large ventrolateral apophysis at about the middle. The apophysis bears a forward-pointing spine distally. The right metatarsus has a thick, heavy, but very small prolateral spine distal to the apophysis. A slightly modified distal spine in the inner ventral row of the tibia.

Investiture. Male. Hair largely rubbed off, but apparently normal in pattern. Tarsi of all but the first pair of legs with ventral scopulae at least distally.

Female. No unusual features.

Spination. See Table 10.

Diagnosis. Male. The single ventral apophysis on the first metatarsus distinguishes *A. gracilis* from all other American species, except possibly *A. obscura* (see discussion above).

Female. The presence of two or three prolateral spines on femur I separates the female from all other American species except *A. multispinosa.* From the latter, *A. gracilis* differs by having lateral tibial spines and fewer ventral tibial spines.

Distribution. Northern Brazil and eastern Peru, in the Amazon Basin and along river valleys in the higher regions (Map 2).

Records. BRAZIL. AMAZONAS: Teffé. PARA: Belem. Caxias, ♂ holotype, St. André. BAHIA: Salvador.

PERU. SAN MARTÍN: Mishqui-Yacu, 20 km NE Moyobamba, 1200 m (3940 ft).

Ariadna obscura (Blackwall)
Map 3.

Dysdera obscura Blackwall, 1858, Ann. Mag. Nat. Hist., 3(2):334. Immature holotype from Brazil, Pernambuco, destroyed. Blackwall, 1861, Ann. Mag. Nat. Hist., 3(48):446; Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:132; Bonnet, 1956, Biblio. Aran., 2(2):1632.

Ariadora [*sic*] *campinensis* Mello-Leitão, 1916, Broteria, 15(1):13. Female holotype from Campina Grande, Paraiba do Norte, in Museu Nacional, Rio de Janeiro, not seen. Mello-Leitão, 1947, Arq. Mus. Paranaense, 6(6):234; Bonnet, 1955, Biblio. Aran., 2(1):732.

Ariadna taperae Mello-Leitão, 1926, Ann. Acad. Brasil. Sci., 1(2):93. Male and female syntypes from "Tapera," in Museu Nacional, Rio de Janeiro, not seen. Mello-Leitao, 1947, Arq. Mus. Paranaense, 6(6):234.

Ariadna obscura: Mello-Leitão, 1947, Arq. Mus. Paranaense, 6(6):234.

Ariadna taperana: Bonnet, 1955, Biblio. Aran., 2(1):737.

Discussion. The placement of these three species is made very difficult by the inaccessibility of all three types and the fact that only one specimen is available from the general region where the types were collected, about 100 miles from the nearest type locality.

Blackwall's description, incomplete and incorrect as it is, suffices to place *Dysdera obscura* in the genus *Ariadna.* It contains nothing, however, which could possibly identify any given species of the genus. The type is not available, and Cooke (in litt.) states that the specimen was probably destroyed before Blackwall's collection came into the Oxford Museum.

In 1947, Mello-Leitão synonymized his own species *campinensis* and *taperae* with *obscura*, without giving any reasons for his action. It is unlikely that he had ever seen an authentic specimen of *obscura.* The synonymy is justifiable on the basis of dis-

tribution, however. All three species, as well as the specimen assigned to *A. obscura* below, originate in a sector of easternmost Brazil about 350 miles (560 km) in diameter. Except for a few insular species, most frequently collected American *Ariadna* have a range far larger than this. The probability that more than one species occupies this part of Brazil seems quite small.

The discrepancies between the descriptions of Mello-Leitão's two species and the specimen from Natal are more serious, although Mello-Leitão offers only a small fraction of the information available from his specimens. The disagreements in numbers of metatarsal spines are relatively unimportant, lying, as they do, within the normal range of variation of a single deme in other species. The tibial spination, and to some extent that of the third metatarsus, offers problems, however. Both *obscura* and *campinensis* are described as having 5–5 or 6–6 ventral spines on tibiae I and II. The specimen from Natal has 4–4 on tibia I and 4–1 on tibia II. An unusually variable species, such as *A. pilifera*, might include all three variants of first tibial spination, but the difference between 4–1 and 6–6 on the second tibia, a leg segment normally showing a highly stable pattern of spination, is far too great for any single species known to me.

Further inspection of Mello-Leitão's descriptions, and comparison with many specimens of other species, suggests that his published data are in error, perhaps seriously so. *Ariadna campinensis*, for example, is described as having 6–6 ventral spines in four areas, the ventral surfaces of tibiae and metatarsi I and II. Examination of 158 specimens of *A. maxima* and *A. bicolor* reveals not a single specimen having such a degree of symmetry or uniformity of spine numbers in all four areas. In fact, I can not locate in my records a single instance of complete symmetry in spination in any mature *Ariadna*.

Almost certainly, therefore, the meager information on spination given by Mello-Leitão is inaccurate. With some reluctance, because of the magnitude of the discrepancies between descriptions and specimen, I conclude that the best course is to regard the three described species as synonymous, and to assume, until otherwise demonstrated, that the specimen on hand is *Ariadna obscura*.

Color. Male. Blackwall (1861) describes the male as generally paler than the female, but with the anterior legs browner, and the palpi yellowish white.

Female. Carapace and legs I and II deep brown. The other legs paler. Sternum, labium, and undersides of coxae only a little lighter than carapace. Abdomen dark gray above, slightly paler beneath.

Structure. Dimensions of one female: total length 8.5 mm; carapace length 4.1 mm; carapace width 2.4 mm; sternum length 2.3 mm; sternum width 1.37 mm.

Male palp. Details of structure unknown.

Male first leg. Described by Blackwall (1861) as having a retrolateral or ventroretrolateral apophysis ending in a short spine.

Investiture. Female. Hair largely rubbed off, but apparently of normal pattern. Lateral spines of tibiae I and II, and prolateral spines of patellae quite short, appressed, and almost invisible against the dark brown leg.

Spination. See Table 16.

Diagnosis. Male. Blackwall's description of the male indicates a similarity to *A. gracilis*, but to no other known male. The data given are insufficient to diagnose *A. obscura* more precisely.

Female. The metatarsal comb of two spines distinguishes *A. obscura* from most other species. From the others with two-spined comb, it may be separated by the presence of spines on the patellae of legs I and II, a unique character in females of American *Ariadna*.

Distribution. Eastern Brazil, in the states of Rio Grande do Norte, Paraiba, Pernambuco, and possibly Bahia.

Records. BRAZIL. RIO GRANDE DO NORTE: Natal, June 1911, Stanford Exp., ♀, (W. M. Mann); PARAIBA: Campina Grande (type locality of *A. campinensis*); PERNAMBUCO: no further data (type locality of *A. obscura*); Tapera (Pernambuco or Bahia?), no further data (type locality of *A. taperae*).

Ariadna solitaria Simon
Map 4.

Ariadne solitaria Simon, 1891, Proc. Zool. Soc. London, 1891:556. Immature holotype from Lesser Antilles, St. Vincent Island, in British Museum (Natural History), examined.

Ariadna solitaria Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):737.

Not *A. solitaria:* Lutz, 1915, Ann. New York Acad. Sci., 26:81 (=*A. arthuri*).

Discussion. Although known only from the immature holotype, this species is clearly distinct from the two other West Indian *Ariadna*, both of which have more ventral tibial spines. No other *Ariadna* has been taken in the Windward Islands or the nearby coast of northern South America. Possibly *A. solitaria* will ultimately prove to have a more extensive range in this region.

Color. Carapace and chelicerae orange-brown, lighter in cephalic region. Legs and palps yellow, tarsus of palp, tarsi of legs I and II, metatarsus of leg I darker. Endites, labium, and sternum yellow. Abdomen grayish yellow above, yellow beneath.

Structure. Dimensions of holotype: Total length 9.0 mm, carapace length 4.2 mm, carapace width 2.0 mm; sternum length 2.1 mm; sternum width 0.979 mm.

Investiture. Largely rubbed off, but apparently plentiful and of usual arrangement.

Spination. See Table 19.

Diagnosis. Lateral spines present on first two tibiae; ventral spines of tibiae I and II 4–4; metatarsal comb of 4 spines. Spination of third leg: 4 ventral, 2 prolateral, 0 retrolateral spines on metatarsus; 2 ventral, no lateral spines on tibia.

Distribution. Thus far found only on St. Vincent, Windward Islands.

Record. ST. VINCENT: Baronallie, near sea-level, open valley, under rubbish, o, (H. H. Smith).

Ariadna tubicola Simon
Map 4.

Ariadne tubicola Simon, 1893, Ann. Soc. Ent. Fr., 61:448. Immature syntypes from Venezuela, Caracas, in Muséum National d'Histoire Naturelle, Paris, examined.

Ariadna tubicola: Petrunkevitch, 1911, Bull. Amer. Mus. Nat. Hist., 29:131; Bonnet, 1955, Biblio. Aran., 2(1):738.

Discussion. The two immature syntypes are the only specimens presently known. They seem to me sufficiently distinct from the other *Ariadna* of northwestern South America to be considered a separate species. Again, many more specimens will be required to establish the status of the form firmly.

Color. Carapace orange, legs yellow. Metatarsi I and II with distal and subbasal dark annuli. Chelicerae, endites, labium, and sternum brownish yellow. Abdomen in poor condition, yellow with a suggestion of a median series of purplish gray markings of the usual form.

Structure. Dimensions of immature lectotype: Total length 7.4 mm, carapace length 3.0 mm, carapace width 1.8 mm, sternum length 1.7 mm, sternum width 1.08 mm.

Investiture. Hair reddish brown, of usual distribution.

Spination. See Table 22.

Diagnosis. Lateral spines present on tibiae I and II; ventral tibial spines more than 4–4 on I and II; metatarsal comb of 4–5 spines; a single prolateral spine on femur I; palpal patella with one prolateral spine; tarsi very short.

Distribution. North central Venezuela (Map 4).

Record. VENEZUELA. DISTRITO FE-

DERAL: Caracas, oo, (E. Simon), syntypes.

Ariadna Incertae Sedis
Map 3.

Ariadna conspersa Mello-Leitão, 1940, Arq. Inst. Biol. Sao Paulo, 11(30):256.
Dysdera crassipalpus Blackwall, 1863, Ann. Mag. Nat. Hist., ser. 3, 11(61):43.
Ariadna dubia Mello-Leitão, 1917, Broteria, 15:82.
Ariadna spinifera Mello-Leitão, 1947, Arq. Museu Paranaense, 6(6):233, figure 1, ♂.

No holotypes or specimens from the type localities of any of these species have been seen. Blackwall's description is worthless, those of Mello-Leitão are so fragmentary, and probably inaccurate, as to be unusable. Two of the species, *crassipalpus* and *dubia*, were described from specimens taken in Rio de Janeiro, a male and a female respectively. The holotypes of *A. spinifera* and *A. conspersa* are a male and a female from Curitiba, Paraná.

Similar situations involving *A. bicolor* and *A. maxima* were readily solved, and it is tempting to apply the same procedure to the present species. Four species described from the United States and four from Chile were reduced to one in each case when study of many specimens from widely scattered localities revealed that the populations in each area were quite uniform. My original inclination, therefore, was to unite all the southeastern Brazilian species under one or, at most, two names. Certainly the description of a male and female from each of the two Brazilian sites suggested each pair of names referred to a single species.

The relatively short airline distance of 400 miles separates Rio de Janeiro and Curitiba. Eight other American *Ariadna*, all the species that are fairly well-known, range over distances much greater than 400 miles. Furthermore, in North America, Central America, and the West Indies the pattern of distribution of *Ariadna* is one of allopatry of all species so far as presently known. This statement is true for most of South America, also, but so few specimens of most species have been collected in South America that the known distribution there is of little significance.

Unfortunately the simple treatment that was appropriate for *A. bicolor* and *A. maxima* can not be justified for the Brazilian species. A small collection of specimens from São Paulo (almost exactly halfway between Rio de Janeiro and Curitiba) has been examined. This collection contains three, or possibly four, species. *Ariadna mollis* has also been collected in southeastern Brazil, and may occur in the São Paulo region.

At present I find the task of matching the available specimens with the published names impossible. Examination of type material would be a step toward solving the problem, but in itself might be insufficient. Series of specimens from several localities, certainly including Rio de Janeiro and Curitiba, will be required. These series must include a number of mature females (five at the minimum), and should also include at least one male from each locality. The material already on hand suggests that some of the species are not very different from each other morphologically.

The region from Buenos Aires, Argentina, to Diamantina in the Brazilian state of Minas Gerais presents more serious taxonomic problems and more interesting biological ones in the genus *Ariadna* than any other part of the Americas. The only indications of sympatry of two or more species of *Ariadna* are in this area and in southern Chile. Besides the situation described above, *A. mollis* and *A. boesenbergii* have apparently been taken together in Buenos Aires, and *A. boliviana* was found with another (undetermined) species at Diamantina. Plainly, on-the-spot investigations at least in southeastern Brazil are needed.

LITERATURE CITED

Banks, N. 1929. Spiders from Panama. Bull. Mus. Comp. Zool., **69**(3):53–96.

Barnes, R. D. 1953. The ecological distribution of spiders in nonforest maritime communities at Beaufort, North Carolina. Ecol. Monographs, **23**:315–337.

Beatty, J. A., and W. H. Bossert. (in prep). A computerized study of American *Ariadna* (Araneae: Dysderidae).

Blackwall, J. 1858. Characters of a new genus and descriptions of three recently discovered species of Araneidea. Ann. Mag. Nat. Hist., ser. 3, **2**:331–335.

———. 1861. Descriptions of several recently discovered spiders. Ann. Mag. Nat. Hist., ser. 3, **8**:441–446.

———. 1863. Descriptions of newly discovered spiders captured in Rio Janeiro by John Gray, Esq., and the Rev. Hamlet Clark. Ann. Mag. Nat. Hist., ser. 3, **11**:29–45.

Bonnet, P. 1955. Bibliographia Araneorum. Toulouse, **2**(1):1–918;

———. 1956. *Op. cit.*, **2**(2):919–1925.

———. 1958. *Op. cit.*, **2**(4):3027–4230.

Bryant, E. B. 1948. Spiders of Hispaniola. Bull. Mus. Comp. Zool., **100**(4):332–447.

Buxton, B. H. 1913. Coxal glands of the arachnids. Zool. Jahrb. Suppl., **14**:231–282.

Chamberlin, R. V. 1916. Results of the Yale Peruvian Expedition of 1911. The Arachnida. Bull. Mus. Comp. Zool., **60**(6):177–299.

———. 1920. South American Arachnida, chiefly from the Guano Islands of Peru. Bull. Brooklyn Inst. Arts Sci., **3**(2):35–44.

———. 1924. The spider fauna of the shores and islands of the Gulf of California. Proc. California Acad. Sci., ser. 4, **12**:561–694.

Chamberlin, R. V., and W. Ivie. 1935. Miscellaneous new American spiders. Bull. Univ. Utah, Biol. Ser., **2**(8):1–79.

Comstock, J. H. 1948. The spider book. 2d ed., rev. W. J. Gertsch. Ithaca, New York: Comstock Publ. Co., p. 306.

Cooke, J. A. L. 1965a. Spider genus *Dysdera* (Araneae, Dysderidae). Nature (London), **205**(4975):1027–1028.

———. 1965b. Systematic aspects of the external morphology of *Dysdera crocata* and *Dysdera erythrina* (Araneae, Dysderidae). Acta Zool., **46**:41–65.

———. 1966. Synopsis of the structure and function of the genitalia in *Dysdera crocata* (Araneae: Dysderidae). Senckenbergiana Biologica, **47**:35–43.

Emerton, J. H. 1875. Notes and descriptions. *In* N. M. Hentz, Descriptions and figures of the Araneides of the United States. Occ. Pap. Boston Soc. Nat. Hist., **2**:15–164.

Franganillo, B. P. 1936. Los Aracnidos de Cuba hasta 1936. La Habana, p. 38.

Gerhardt, U. 1921. Vergleichende Studien über die Morphologie des männlichen Tasters und die Biologie der Kopulation der Spinnen. Arch. Naturg., **87**:78–247.

Gerhardt, U., and A. Kastner. 1938. Araneae — Echte Spinnen — Webspinnen. *In* W. Kükenthal and T. Krumbach, Handbuch der Zoologie, **3**(2):497–656.

Gertsch, W. J. 1958a. The spider family Diguetidae. Amer. Mus. Novitates, **1904**: 1–24.

———. 1958b. The spider genus *Loxosceles* in North America, Central America, and the West Indies. Amer. Mus. Novitates, **1907**: 1–46.

———. 1958c. The spider family Plectreuridae. Amer. Mus. Novitates, **1920**:1–53.

———. 1967. The spider genus *Loxosceles* in South America. Bull. Amer. Mus. Nat. Hist., **136**(3):121–173.

Kaston, B. J. 1948. Spiders of Connecticut. State Geo. Nat. Hist. Survey, Connecticut, **70**:48.

———. 1952. How to Know the Spiders. Dubuque, Iowa: Wm. C. Brown Co., p. 25.

Lutz, F. E. 1915. List of Greater Antillean spiders with notes on their distribution. Ann. New York Acad. Sci., **26**:71–148.

Mello-Leitão, C. de. 1916. Notas Arachnologicas. IV. Novas especies do Brasil. Broteria, **14**:12–13.

———. 1917. Notas Arachnologicas. V. Especies novas ou pouco conhecidas do Brasil. Broteria, **15**:74–102.

———. 1933. Catalogo das aranhas argentinas. Arch. Esc. Sup. Agric. Med. Vet., **10**(1): 3–63.

———. 1940. Aranhas do Paraná. Arq. Inst. Biol. (Sao Paulo), **11**(30):235–257.

———. 1941. Las arañas de Córdoba, La Rioja, Catamarca, Tucumán, Salta y Jujuy. Rev. Mus. La Plata, N. S., Secc. Zool., **2**:99–198.

———. 1944. Catalogo das aranhas do Rio Grande do Sul. Arq. Mus. Nac., (Rio de Janeiro), **37**:149–245.

———. 1945. Arañas de Misiones, Corrientes y Entre Rios. Rev. Mus. La Plata, N. S., Secc. Zool., **4**:213–302.

———. 1946. Arañas del Paraguay. Not. Mus. La Plata, N. S., Secc. Zool., **11**:17–50.

———. 1947. Aranhas do Parana e Santa Catarina, das Colecões do Museu Paranaense. Arq. Mus. Paranaense, **6**(6):231–304.

Millot, J. 1931. Anatomie comparée de l'intestin moyen céphalo-thoracique chez les Araignées vraies. Zeits. Morph. Okol. Tiere, **21**:740–764.

Petrunkevitch, A. 1911. A synonymic index-catalogue of spiders of North, Central and South America with all adjacent islands. Bull. Amer. Mus. Nat. Hist., **29**:130–132.

———. 1926. Spiders from the Virgin Islands.

Trans. Connecticut Acad. Arts Sci., **28**:21–78.
———. 1929. The spiders of Porto Rico. Part one. Trans. Connecticut Acad. Arts Sci., **30**:1–158.
———. 1933. An inquiry into the natural classification of spiders, based on a study of their internal anatomy. Trans. Connecticut Acad. Arts Sci., **31**:303–389.
———. 1939. Classification of the Araneae, with key to suborders and families. Trans. Connecticut Acad. Arts Sci., **33**:133–190.
Pickard-Cambridge, O. 1898. Biologia Centrali-Americana, Arachnida, Araneidea. London, **1**:235.
Porter, C. E. 1917. Apuntes sobre aracnologia chilena. I. Sinopsis de los Disdéridos. Rev. Chilena Hist. Nat., **21**(6):172–182.
Purcell, W. F. 1904. Descriptions of new genera and species of South African spiders. Trans. South African Phil. Soc., **15**(3):115–173.
Simon, E. 1891. On the spiders of the island of St. Vincent. Part 1. Proc. Zool. Soc. London, **1891**:549–575.
———. 1893a. Histoire naturelle des Araignées. Paris, **2**:308–322.
———. 1893b. Arachnides. *In* Voyage de M. E. Simon au Venezuela (Décembre 1887-Avril 1888). 21e Mémoire. Ann. Soc. Ent. Fr., **61**:423–462.
Snodgrass, R. E. 1935. Principles of Insect Morphology. New York: McGraw-Hill Co., pp. 56–57.
Suzuki, S. 1952. Cytological studies in spiders, III. Jour. Sci. Hiroshima Univ., (Zool.), **15**:23–136.
Wigglesworth, V. B. 1954. The Physiology of Insect Metamorphosis. Cambridge: Cambridge University Press, pp. 52–54.

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ADDENDUM

Since this work was completed, additional specimens have become available through the cooperation of Dr. W. J. Gertsch and Mr. Vincent Roth, of the American Museum of Natural History. One of these specimens is the first known male of *Ariadna fidicina* (originally *Citharoceps fidicina*). It has the stridulating patches on the carapace, as in the female. Other structural characters agree with the definition of *Ariadna*, confirming the synonymy of *Citharoceps* with *Ariadna*, as expected.

The remaining new material consists of one male, many mature females, and a few juveniles of *A. tarsalis*, collected on several of the Galapagos Islands. Mature *Ariadna* from the Galapagos have not previously been available to me. These specimens agree in all respects with those described above as *Ariadna peruviana*, new species. Therefore *A. peruviana* is hereby synonymized with *A. tarsalis* Banks. The presence of *A. tarsalis* on the mainland of South America is unexpected and surprising. However, a coastal species at Lima is admirably placed for rafting to the Galapagos on the Humboldt Current.

A later paper will give details on the above specimens, with illustrations, and with modifications of the descriptions and keys for *A. tarsalis* and *A. fidicina*.

TABLE 2. SPINATION OF *ARIADNA PERUVIANA*

		Male N = 4			Female N = 11–12		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	4	0	0	12
	Tibia	0	0	4	3–5	3	6
	Tarsus	0	0	4	6–8	6	6
Leg:							
1—Meta.—Ventral ou.		1	1	4	8–10	9	7
Ventral in.		2	2	4	8–10	9	5
Prolateral		0–1	0	3	0	0	11
Tibia—Ventral ou.		4–6	4	3	4–6	4	14
Ventral in.		4	4	4	4–5	4	10
Ventral su.		0–1	0, 1	2 ea.	0	0	11
Dorsal		1	1	4	0	0	11
Femur—Dorsal ou.		1	1	4	1	1	11
Dorsal mi.		2	2	4	1–2	1	10
Dorsal in.		1–2	2	3	0–2	1	8
Prolateral		1	1	4	1	1	11
2—Meta.—Ventral ou.		3	3	4	7–10	9	7
Ventral in.		3	3	4	9–11	9	6
Prolateral		1–2	1	3	0	0	11
Retrolateral		3	3	4	0	0	11
Tibia—Ventral ou.		4	4	4	3–5	4	6
Ventral in.		1–2	1, 2	2 ea.	4	4	11
Prolateral		3	3	4	2–3	3	10
Retrolateral		4	4	4	2–3	3	8
Dorsal		0–1	1	3	0	0	11
Femur—Dorsal ou.		2	2	4	0–1	1	10
Dorsal mi.		4	4	4	1–4	1	6
Dorsal in.		1–2	2	3	1–2	1	7
3—Meta.—Ventral ou.		3	3	4	3	3	12
Ventral in.		2	2	4	2	2	12
Prolateral		4	4	4	3–4	4	8
Retrolateral		2–3	2, 3	2 ea.	0–3	1	6
Tibia—Ventral ou.		3–5	3	3	3	3	12
Ventral in.		1–2	1	3	0–2	0	10
Prolateral		2	2	4	1–2	2	11
Retrolateral		1–3	1, 3	2 ea.	0	0	12
Femur—Dorsal ou.		0–2	1	2	0	0	12
Dorsal mi.		3–5	3	2	0–3	0	6
Dorsal in.		2	2	4	1–2	2	9
4—Meta.—Ventral ou.		2–3	2, 3	2 ea.	1–2	1	8
Ventral in.		3–4	3	3	3–4	3	9
Ventral su.		1	1	4	0–1	1	7
Tibia—Ventral ou.		0–1	0, 1	2 ea.	0–1	0	10
Ventral in.		0–1	0	3	0	0	12
Retrolateral		1–2	1, 2	2 ea.	0–1	0	10
Femur—Dorsal ou.		0	0	4	0	0	12
Dorsal mi.		7–11		1 ea.	0–4	2	6
Dorsal in.		0–2	2	2	0–1	0	11

Table 3. Spination of *Ariadna arthuri*

		Male N = 4			Female N = 9–10		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	4	0	0	9
	Tibia	0	0	4	4–9	4	5
	Tarsus	0	0	4	5–8	6, 7	3 ca.
Leg:							
1—Meta.—	Ventral ou.	2	2	4	6–9	7	4
	Ventral in.	3	3	4	6–8	7, 8	4 ca.
Tibia—	Ventral ou.	7	7	4	5–8	6	4
	Ventral in.	1–2	1, 2	2 ea.	4–6	6	7
	Prolateral	3	3	4	2–3	3	6
	Retrolateral	3	3	4	2	2	10
	Dorsal	1	1	4	0	0	10
Femur—	Dorsal ou.	1	1	4	1	1	10
	Dorsal mi.	1–2	1, 2	2 ea.	1	1	10
	Dorsal in.	2	2	4	1–2	2	6
	Prolateral	0–1	0, 1	2 ea.	1	1	10
2—Meta.—	Ventral ou.	4	4	4	6–9	7	5
	Ventral in.	3	3	4	7–8	8	8
	Retrolateral	2	2	4	0	0	10
Tibia—	Ventral ou.	7	7	4	6–8	7	5
	Ventral in.	1	1	4	4–7	6	7
	Ventral su.	0–1	0, 1	2 ea.	0	0	10
	Prolateral	3	3	4	1–3	3	6
	Retrolateral	4	4	4	1–2	2	9
	Dorsal	0–1	0	3	0	0	10
Femur—	Dorsal ou.	1	1	4	1	1	10
	Dorsal mi.	1–2	2	3	0–1	1	7
	Dorsal in.	2	2	4	1–2	2	6
3—Meta.—	Ventral ou.	3	3	4	3	3	10
	Ventral in.	1	1	4	1	1	10
	Prolateral	2	2	4	0–3	0	4
	Retrolateral	2	2	4	0	0	10
Tibia—	Ventral ou.	3	3	4	2–3	3	9
	Ventral in.	0	0	4	0	0	10
	Retrolateral	2–3	2, 3	2 ea.	1–2	1	9
Femur—	Dorsal ou.	1	1	4	0–1	1	6
	Dorsal mi.	0–3		1 ea.	0	0	10
	Dorsal in.	1	1	4	0–1	0	6
4—Meta.—	Ventral ou.	1	1	4	1	1	10
	Ventral in.	2	2	4	2	2	10
	Ventral su.	1	1	4	0	0	10
Femur—	Dorsal ou.	0	0	4	0	0	10
	Dorsal mi.	2–5	5	2	0	0	10
	Dorsal in.	0–1	0, 1	2 ea.	0	0	10

TABLE 4. SPINATION OF *ARIADNA BICOLOR*

		Male N = 100			Female N = 200		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	100	0–1	0	198
	Tibia	0	0	100	0–6	3	139
	Tarsus	0	0	100	5–16	9	53
Leg:							
1—Meta.—Ventral ou.		2–3	2	97	6–11	8	107
Ventral in.		3–4	3	96	7–11	8	100
Tibia—Ventral ou.		3–5	4	97	3–6	4	184
Ventral in.		2–5	4	86	2–6	4	165
Prolateral		0–5	4	46	0	0	200
Retrolateral		0–5	4	79	0	0	200
Femur—Dorsal ou.		0–2	1	90	0–1	0	199
Dorsal mi.		1–6	3	24	0–2	0	194
Dorsal in.		0–2	2	55	0–2	0	162
2—Meta.—Ventral ou.		2–4	3	97	5–12	8	103
Ventral in.		2–7	3	95	7–12	9	88
Prolateral		0–3	1	45	0	0	200
Retrolateral		0–2	2	82	0	0	200
Tibia—Ventral ou.		3–6	4	90	3–5	4	190
Ventral in.		1–2	2	97	0–4	2	188
Prolateral		0–5	3	46	0	0	200
Retrolateral		0–5	3	33	0	0	200
Femur—Dorsal ou.		0–2	1	66	0	0	200
Dorsal mi.		0–5	4	42	0–2	0	195
Dorsal in.		0–3	1	68	0–2	1	167
3—Meta.—Ventral ou.		2–4	3	96	2–6	3	186
Ventral in.		0–2	1	94	0–3	1	189
Prolateral		0–5	2	54	1–4	2	160
Retrolateral		0–2	0	92	0	0	200
Tibia—Ventral ou.		1–6	4	44	0–4	2	99
Ventral in.		0–3	1	52	0	0	200
Prolateral		0–4	1	44	0–1	0	181
Femur—Dorsal ou.		0	0	100	0	0	200
Dorsal mi.		0–5	3	48	0–1	0	199
Dorsal in.		0–2	1	85	0–2	1	101
4—Meta.—Ventral ou.		1–3	2	81	0–2	1	170
Ventral in.		3–5	3	91	2–4	3	191
Prolateral		0–3	2	64	0	0	200
Tibia—Ventral ou.		0–4	2	28	0	0	200
Femur—Dorsal ou.		0	0	100	0	0	200
Dorsal mi.		1–8	3	40	0	0	200
Dorsal in.		0–2	1	53	0	0	200

Table 5. Spination of *Ariadna boesenbergi*

		Male N = 2			Female N = 7–8		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	2	0	0	8
	Tibia	0	0	2	2–4	3, 4	3 ea.
	Tarsus	0	0	2	4–6	5	4
Leg:							
1—Meta.—Ventral ou.		3, 4		1 ea.	5–9	8	3
Ventral in.		4	4	2	6–8	7	3
Prolateral		1	1	2	0	0	7
Retrolateral		2	2	2	0	0	7
Tibia—Ventral ou.		4, 6		1 ea.	4	4	7
Ventral in.		4	4	2	4	4	7
Prolateral		3, 4		1 ea.	0	0	7
Retrolateral		6	6	2	0	0	7
Femur—Dorsal ou.		1	1	2	0	0	7
Dorsal mi.		2, 3		1 ea.	0–1	0	6
Dorsal in.		2	2	2	0–1	0	6
2—Meta.—Ventral ou.		3	3	2	6–9	7	4
Ventral in.		4	4	2	6–8	7	4
Prolateral		1	1	2	0	0	8
Retrolateral		2	2	2	0	0	8
Tibia—Ventral ou.		4	4	2	4–5	4	7
Ventral in.		4	4	2	3–4	4	6
Ventral su.		1	1	2	0	0	8
Prolateral		4	4	2	0	0	8
Retrolateral		5, 6		1 ea.	0	0	8
Femur—Dorsal ou.		2	2	2	0	0	8
Dorsal mi.		2, 3		1 ea.	0–1	0	6
Dorsal in.		2	2	2	0–2	2	4
3—Meta.—Ventral ou.		3	3	2	2–3	3	6
Ventral in.		2	2	2	1	1	8
Prolateral		3	3	2	1–2	1	5
Tibia—Ventral ou.		4	4	2	1–4	3	5
Prolateral		2	2	2	0	0	8
Retrolateral		1	1	2	0	0	8
Femur—Dorsal ou.		0	0	2	0	0	8
Dorsal mi.		3	3	2	0	0	8
Dorsal in.		1, 2		1 ea.	0–1	1	6
4—Meta.—Ventral ou.		2	2	2	1	1	7
Ventral in.		4	4	2	4	4	7
Tibia—Ventral ou.		2, 3		1 ea.	0	0	7
Femur—Dorsal ou.		0	0	2	0	0	7
Dorsal mi.		8, 9		1 ea.	0	0	7
Dorsal in.		1	1	2	0–1	0	5

TABLE 6. SPINATION OF *ARIADNA BOLIVIANA*

		Male N = 4			Female N = 2		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	4	1	2	2
	Tibia	0	0	4	6	6	2
	Tarsus	0	0	4	10	10	2
Leg:							
1—Meta.—Ventral ou.		1–2	1, 2	2 ea.	7, 8		1 ea.
Ventral in.		2–3	2, 3	2 ea.	8	8	2
Tibia—Ventral ou.		4	4	4	4	4	2
Ventral in.		1–2	1, 2	2 ea.	4, 5		1 ea.
Ventral su.		0–1	0, 1	2 ea.	0	0	2
Prolateral		3–4	3, 4	2 ea.	3	3	2
Retrolateral		7–8	7, 3	2 ea.	3	3	2
Dorsal		1–2	1	3	0	0	2
Femur—Dorsal ou.		1	1	4	1	1	2
Dorsal mi.		3–4	4	3	1	1	2
Dorsal in.		1–2	2	3	2	2	2
Prolateral		1?	1?	4	1	1	2
2—Meta.—Ventral ou.		3–4	3	3	7, 8		1 ea.
Ventral in.		2	2	4	8, 9		1 ea.
Retrolateral		2	2	4	1	1	2
Tibia—Ventral ou.		4	4	4	4, 5		1 ea.
Ventral in.		1–2	1, 2	2 ea.	3	3	2
Ventral su.		1	1	4	0	0	2
Prolateral		3	3	4	3	3	2
Retrolateral		4–5	4, 5	2 ea.	3, 4		1 ea.
Dorsal		0–1	1	3	0	0	2
Femur—Dorsal ou.		1	1	4	1	1	2
Dorsal mi.		3–4	4	3	1	1	2
Dorsal in.		1–2	1, 2	2 ea.	2	2	2
3—Meta.—Ventral ou.		3	3	4	3	3	2
Ventral in.		1–2	1, 2	2 ea.	2, 3		1 ea.
Prolateral		2–3	2, 3	2 ea.	3, 4		1 ea.
Retrolateral		2	2	4	1, 2		1 ea.
Tibia—Ventral ou.		3–4	3	3	3	3	2
Prolateral		2	2	4	1, 2		1 ea.
Retrolateral		2–3	2	3	1	1	2
Femur—Dorsal ou.		0–1	1	3	1	1	2
Dorsal mi.		2–4	3	2	1	1	2
Dorsal in.		1–2	3	2	1	1	2
4—Meta.—Ventral ou.		0–1	0, 1	2 ea.	0	0	2
Ventral in.		4–5	4	3	3, 4		1 ea.
Femur—Dorsal ou.		0	0	4	0	0	2
Dorsal mi.		2–5		1 ea.	0	0	2
Dorsal in.		0–1	0, 1	2 ea.	0	0	2

Table 7. Spination of *Ariadna caerulea*

		Male N = 2			Female N = 11–12		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	2	0	0	12
	Tibia	0	0	2	3–5	3	6
	Tarsus	0	0	2	4–11	5	5
Leg:							
1—Meta.—Ventral ou.		1	1	1	8–11	8, 10	5 ea.
Ventral in.		1	1	1	8–11	8, 9	4 ea.
Tibia—Ventral ou.		6	6	1	4–6	4	7
Ventral in.		1	1	1	4–7	7	8
Prolateral		4	4	1	0–3	2	6
Retrolateral		4	4	1	0–2	2	5
Femur—Dorsal ou.		2	2	1	0–1	1	10
Dorsal mi.		4	4	1	0–1	1	11
Dorsal in.		1	1	1	1–2	2	10
Prolateral		1	1	1	1	1	12
2—Meta.—Ventral ou.		2	2	2	7–10	7–9	3 ea.
Ventral in.		3	3	2	8–11	9	5
Retrolateral		0–1	0, 1	1 ea.	0	0	11
Tibia—Ventral ou.		6	6	2	4–7	4	6
Ventral in.		2–3	2, 3	1 ea.	3–4	4	9
Ventral su.		0–1	0, 1	1 ea.	0	0	11
Prolateral		3–4	3, 4	1 ea.	0–3	3	4
Retrolateral		4	4	2	0–3	0	8
Dorsal		1–2	1, 2	1 ea.	0	0	11
Femur—Dorsal ou.		2	2	2	0–1	1	8
Dorsal mi.		3–4	3, 4	1 ea.	1	1	11
Dorsal in.		1–2	1, 2	1 ea.	1	1	11
3—Meta.—Ventral ou.		3	3	1	3	3	12
Ventral in.		1	1	1	0–2	1	7
Prolateral		4	4	1	0–3	2	6
Retrolateral		2	2	1	0	0	12
Tibia—Ventral ou.		4	4	1	2–3	3	7
Ventral in.		1	1	1	0	0	12
Prolateral		2	2	1	0–1	0	9
Retrolateral		3	3	1	0–2	0	10
Femur—Dorsal ou.		1	1	1	0–1	0	11
Dorsal mi.		4	4	1	0	0	12
Dorsal in.		1	1	1	0–1	1	10
4—Meta.—Ventral ou.		2–3	2, 3	1 ea.	0–1	0	7
Ventral in.		3	3	2	3–4	4	9
Prolateral		0–1	0, 1	1 ea.	0	0	11
Tibia—Ventral ou.		1	1	2	0	0	11
Femur—Dorsal ou.		0	0	2	0	0	11
Dorsal mi.		3–5	3, 5	1 ea.	0	0	11
Dorsal in.		1	1	2	0	0	11

TABLE 8. SPINATION OF *ARIADNA CEPHALOTES*

		Female N = 15–18		
		Range	Mode	n
Palp	Patella	0	0	17
	Tibia	2–5	3	13
	Tarsus	5–15	8	5
Leg:				
1—Meta.—	Ventral ou.	7–11	10	7
	Ventral in.	6–11	9	8
Tibia—	Ventral ou.	4–7	4	14
	Ventral in.	4–5	4	16
	Retrolateral	0–4	0	11
Femur—	Prolateral	1	1	17
2—Meta.—	Ventral ou.	7–11	9	5
	Ventral in.	6–10	8	7
Tibia—	Ventral ou.	4–6	4	14
	Ventral in.	3–4	3	14
Femur—	Dorsal ou.	0	0	16
	Dorsal mi.	0	0	16
	Dorsal in.	0–2	0	14
3—Meta.—	Ventral ou.	3	3	18
	Ventral in.	1	1	18
	Prolateral	1–2	1	12
	Retrolateral	0–2	0	15
Tibia—	Ventral ou.	2–3	3	13
Femur—	Dorsal ou.	0	0	18
	Dorsal mi.	0	0	18
	Dorsal in.	0–2	0	16
4—Meta.—	Ventral ou.	1	1	18
	Ventral in.	3–4	4	16

TABLE 9. SPINATION OF *ARIADNA FIDICINA*

		Female N = 14–20		
		Range	Mode	n
Palp	Patella	0	0	20
	Tibia	3–5	5	11
	Tarsus	7–13	11	5
Leg:				
1—Meta.—	Ventral ou.	4–6	5	16
	Ventral in.	5–7	5	10
	Ventral su.	2	2	18
Tibia—	Ventral ou.	4	4	18
	Ventral in.	3–4	4	17
Femur—	Prolateral	1	1	18
2—Meta.—	Ventral ou.	3–5	4, 5	8 ea.
	Ventral in.	4–6	4	10
	Ventral su.	2	2	17
Tibia—	Ventral ou.	4	4	17
	Ventral in.	0–1	0	12
Femur—	Dorsal ou.	0	0	17
	Dorsal mi.	0	0	17
	Dorsal in.	0–1	0	16
3—Meta.—	Ventral ou.	3	3	19
	Ventral in.	1–2	1	16
	Ventral su.	1–2	1	18
	Prolateral	1–2	1	18
Tibia—	Ventral ou.	1–3	3	14
Femur—	Dorsal ou.	0	0	19
	Dorsal mi.	0	0	19
	Dorsal in.	0–1	0	18
4—Meta.—	Ventral ou.	1–2	1	12
	Ventral in.	4–6	5	15
Tibia—	Ventral ou.	0–2	0	17
	Ventral in.	0–2	0	10

Table 10. Spination of *Ariadna gracilis*

		Male N = 2			Female N = 23–26		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	2	0–2	0	19
	Tibia	1	1	2	6–10	7	9
	Tarsus	0	0	2	7–12	9	8
Leg:							
1—Meta.—	Ventral ou.	1	1	2	7–10	8	11
	Ventral in.	2	2	2	7–10	9	11
	Prolateral	0–1	0, 1	1 ea.	0	0	23
Tibia—	Ventral ou.	6	6	2	6–7	6	21
	Ventral in.	2	2	2	6–7	6	19
	Prolateral	3	3	2	2–3	3	19
	Retrolateral	4	4	2	2–3	2	22
Femur—	Dorsal ou.	1	1	2	1	1	23
	Dorsal mi.	4	4	2	1–2	2	13
	Dorsal in.	2	2	2	1–2	2	22
	Prolateral	0	0	2	2–3	2	17
2—Meta.—	Ventral ou.	3	3	2	7–9	8	16
	Ventral in.	3	3	2	7–11	8, 9	10 ea.
	Retrolateral	1	1	2	0	0	24
Tibia—	Ventral ou.	4	4	2	5–8	6	11
	Ventral in.	2	2	2	5–7	5	16
	Prolateral	3	3	2	2–3	3	19
	Retrolateral	4	4	2	2	2	24
Femur—	Dorsal ou.	1	1	2	1	1	24
	Dorsal mi.	3–4	3, 4	1 ea.	1–2	1	13
	Dorsal in.	2	2	2	1–2	2	23
3—Meta.—	Ventral ou.	3	3	2	3–4	3	24
	Ventral in.	1	1	2	1	1	26
	Prolateral	3	3	2	2–3	3	25
Tibia—	Ventral ou.	2–3	2, 3	1 ea.	1–2	2	22
	Prolateral	2	2	2	0–1	0	19
	Retrolateral	1–2	1, 2	1 ea.	0–1	0	25
Femur—	Dorsal ou.	1–2	1, 2	1 ea.	1–2	1	22
	Dorsal mi.	3–4	3, 4	1 ea.	0–1	0	23
	Dorsal in.	2	2	2	1–2	1	23
4—Meta.—	Ventral ou.	0	0	2	0	0	26
	Ventral in.	4	4	2	3–4	4	21
Femur—	Dorsal ou.	0	0	2	0	0	26
	Dorsal mi.	8	8	2	0	0	26
	Dorsal in.	1	1	2	0	0	26

Table 11. Spination of *Ariadna isthmica*

		Male N = 5–6			Female N = 11–14		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	0	0–1	1	13
	Tibia	0	0	0	4–7	6, 7	5 ea.
	Tarsus	0	0	0	7–11	8	6
Leg:							
1—Meta.—Ventral ou.		2	2	5	6–8	7	8
Ventral in.		2–3	3	4	6–8	7	10
Prolateral		0–1	0	3	0	0	12
Tibia—Ventral ou.		4	4	5	4–5	4	11
Ventral in.		1–2	1	3	3–4	4	11
Ventral su.		0–1	1	3	0	0	12
Prolateral		3–4	3	4	3	3	12
Retrolateral		3–7	3, 5	2 ea.	3	3	12
Dorsal		0–1	0	3	0	0	12
Femur—Dorsal ou.		1	1	5	1	1	12
Dorsal mi.		1–2	2	3	1	1	12
Dorsal in.		2	2	5	1	1	12
Prolateral		0	0	5	1	1	12
2—Meta.—Ventral ou.		3	3	5	6–8	7	9
Ventral in.		3	3	5	6–9	7, 8	5 ea.
Prolateral		0–1	0	3	0	0	12
Retrolateral		0–1	1	3	0	0	12
Tibia—Ventral ou.		4–5	4	4	4–5	4	9
Ventral in.		1–2	2	3	4–5	4	11
Ventral su.		1	1	5	0	0	12
Prolateral		3	3	5	2–3	3	11
Retrolateral		3–4	4	4	2–3	3	8
Dorsal		0–1	0	4	0	0	12
Femur—Dorsal ou.		1	1	5	1	1	12
Dorsal mi.		1–3	3	3	0–1	1	11
Dorsal in.		1–2	2	3	1–2	1	7
3—Meta.—Ventral ou.		3	3	5	3	3	11
Ventral in.		2	2	5	1–2	2	9
Prolateral		2–3	3	4	2–3	3	10
Retrolateral		0–2	0	3	0	0	11
Tibia—Ventral ou.		3	3	5	2–4	3	9
Ventral in.		0–1	0	4	0	0	11
Prolateral		1–2	2	4	0–2	2	8
Retrolateral		2–3	3	4	0–1	0	9
Femur—Dorsal ou.		0–2	1	3	0–1	1	10
Dorsal mi.		2–4	3	3	0	0	13
Dorsal in.		1–2	1	3	0–2	1	10
4—Meta.—Ventral ou.		0–1	1	4	1	1	14
Ventral in.		4	4	5	3–4	4	13
Femur—Dorsal ou.		0	0	5	0	0	14
Dorsal mi.		1–3	1	3	0	0	14
Dorsal in.		0	0	5	0	0	14

Table 12. Spination of *Ariadna maxima*

		Male N = 27–30			Female N = 200		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	30	0–3	1	173
	Tibia	0	0	30	1–6	4	138
	Tarsus	0	0	30	4–9	6	111
Leg:							
1—Meta.—	Ventral ou.	2–4	3	15	6–16	10	53
	Ventral in.	2–8	5	12	8–16	11	55
	Prolateral	0–2	1	13	0	0	200
	Retrolateral	0–9	3	11	0	0	200
	Dorsal	0–5	0	22	0	0	200
Tibia—	Ventral ou.	3–5	4	23	3–6	4	184
	Ventral in.	3–4	4	26	3–5	4	185
	Ventral su.	0–3	1	19	0	0	200
	Prolateral	3–7	4, 5	8 ea.	0–3	3	95
	Retrolateral	9–16	11	8	0–4	3	100
	Dorsal	0–5	0	20	0	0	200
Femur—	Dorsal ou.	1–3	1	18	0–2	1	182
	Dorsal mi.	0–4	1	16	0–2	1	170
	Dorsal in.	1–3	2	21	1–3	2	179
	Prolateral	0–1	1	19	0–1	1	197
2—Meta.—	Ventral ou.	3–5	3	18	6–15	9	49
	Ventral in.	3–7	5	10	7–15	11	48
	Prolateral	0–2	1	23	0	0	200
	Retrolateral	1–10	5	7	0	0	200
	Dorsal	0–2	0	21	0	0	200
Tibia—	Ventral ou.	4–6	4	23	4–7	4	189
	Ventral in.	4	4	27	3–4	4	195
	Prolateral	2–6	3	12	0–3	2	85
	Retrolateral	8–14	11	7	0–3	1	90
	Dorsal	0–3	0	22	0	0	200
Femur—	Dorsal ou.	1–3	2	17	0–2	1	175
	Dorsal mi.	1–7	3, 4	8 ea.	0–2	1	158
	Dorsal in.	1–2	2	25	1–3	1	186
3—Meta.—	Ventral ou.	3–4	3	24	2–4	3	194
	Ventral in.	1–2	2	25	1–2	2	148
	Prolateral	3–4	3	26	1–4	3	184
	Retrolateral	1–4	3	12	0	0	200
Tibia—	Ventral ou.	3–6	3	20	1–4	2	189
	Ventral in.	1–3	1	24	0	0	200
	Prolateral	2–4	2	23	0–3	2	149
	Retrolateral	3–10	5	8	0–2	0	134
Femur—	Dorsal ou.	1–3	2	13	0–1	0	189
	Dorsal mi.	3–6	5	13	0–1	0	197
	Dorsal in.	1–2	2	26	0–2	1	120
4—Meta.—	Ventral ou.	1–3	2	23	0–3	1	174
	Ventral in.	3–4	4	28	4–5	4	199
	Ventral su.	0–1	0	25	0	0	200
	Prolateral	1–6	5	10	0	0	200
	Retrolateral	1–3	2	24	0	0	200
	Dorsal	0–2	0	26	0	0	200
Tibia—	Ventral ou.	0–3	1	17	0	0	200
	Ventral in.	0–2	1	26	0	0	200
	Prolateral	0–1	0	26	0	0	200
	Retrolateral	1–3	1	14	0	0	200
Femur—	Dorsal ou.	0–1	0	28	0	0	200
	Dorsal mi.	0	0	30	0–2	0	187
	Dorsal in.	0–2	1	19	0	0	200

TABLE 13. SPINATION OF *ARIADNA MOLLIS*

		Male N = 2			Female N = 16–18		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	2	0–1	1	13
	Tibia	0	0	2	3–6	5	12
	Tarsus	0	0	2	6–9	6	6
Leg:							
1—Meta.—Ventral ou.		2	2	2	7–11	8	5
Ventral in.		2–3	2, 3	1 ea.	8–11	8	7
Tibia—Ventral ou.		4–5	4, 5	1 ea.	3–4	4	15
Ventral in.		0–2	0, 2	1 ea.	2–4	4	15
Ventral su.		1	1	2	0–1	0	13
Prolateral		2–4	2, 4	1 ea.	2–3	2	11
Retrolateral		4	4	2	0–2	0	7
Dorsal		3	3	2	0	0	17
Pat'l—Prolateral		1	1	2	0	0	17
Femur—Dorsal ou.		1	1	2	0–1	1	16
Dorsal mi.		1	1	2	1	1	17
Dorsal in.		1–2	1, 2	1 ea.	2	2	17
Prolateral		0	0	2	1	1	17
2—Meta.—Ventral ou.		3	3	2	7–11	8	5
Ventral in.		3	3	2	8–11	9	7
Retrolateral		1–2	1, 2	1 ea.	0	0	17
Tibia—Ventral ou.		4–5	4, 5	1 ea.	4	4	18
Ventral in.		3	3	2	2–3	3	17
Ventral su.		1	1	2	0	0	18
Prolateral		3–4	3, 4	1 ea.	1–3	3	12
Retrolateral		4–5	4, 5	1 ea.	0	0	18
Dorsal		1	1	2	0	0	18
Pat'l—Prolateral		0–1	0, 1	1 ea.	0	0	18
Femur—Dorsal ou.		1	1	2	0–1	1	12
Dorsal mi.		3	3	2	1–2	1	17
Dorsal in.		1	1	2	1–2	2	15
3—Meta.—Ventral ou.		3	3	2	3	3	17
Ventral in.		1	1	2	1–2	2	9
Prolateral		2	2	2	2–4	3	12
Retrolateral		2	2	2	0	0	17
Tibia—Ventral ou.		3	3	2	1–3	3	10
Prolateral		1	1	2	0–3	2	10
Retrolateral		0	0	2	0–1	0	16
Femur—Dorsal ou.		0	0	2	0–1	0	15
Dorsal mi.		4–5	4, 5	1 ea.	0–2	1	8
Dorsal in.		1	1	2	0–1	1	16
4—Meta.—Ventral ou.		1	1	2	1	1	17
Ventral in.		7	7	2	5–8	6	13
Femur—Dorsal ou.		0	0	2	0	0	17
Dorsal mi.		5	5	2	0–2	0	8
Dorsal in.		0–1	0, 1	1 ea.	0	0	17

Table 14. Spination of *Ariadna multispinosa*

		Female N = 2	
		Range	n
Palp	Patella	0	2
	Tibia	3	2
	Tarsus	4	2
Leg:			
1—Meta.—	Ventral ou.	9–10	1 ea.
	Ventral in.	10	2
Tibia—	Ventral ou.	11	2
	Ventral in.	8–10	1 ea.
Femur—	Dorsal ou.	1	2
	Dorsal mi.	0–1	1 ea.
	Dorsal in.	0	2
	Prolateral	2–3	1 ea.
2—Meta.—	Ventral ou.	7–8	1 ea.
	Ventral in.	8–10	1 ea.
Tibia—	Ventral ou.	10–11	1 ea.
	Ventral in.	8	2
Femur—	Dorsal ou.	0–1	1 ea.
	Dorsal mi.	1	2
	Dorsal in.	0–1	2
3—Meta.—	Ventral ou.	3	2
	Ventral in.	2	2
	Prolateral	1	2
Tibia—	Ventral ou.	3	2
4—Meta.—	Ventral ou.	0	2
	Ventral in.	4	2

Table 15. Spination of *Ariadna murphyi*

		Female N = 12–14		
		Range	Mode	n
Palp	Patella	0	0	14
	Tibia	0–3	2	6
	Tarsus	3–8	4	4
Leg:				
1—Meta.—	Ventral ou.	4–9	7	6
	Ventral in.	6–9	8	6
Tibia—	Ventral ou.	4	4	12
	Ventral in.	4	4	12
	Prolateral	1–5	3	5
	Retrolateral	0–5	4	5
Femur—	Dorsal ou.	0–1	1	10
	Dorsal mi.	0–3	1	6
	Dorsal in.	0–2	0	6
	Prolateral	1	1	12
2—Meta.—	Ventral ou.	4–9	6, 8	4 ea.
	Ventral in.	6–10	7	5
Tibia—	Ventral ou.	4	4	14
	Ventral in.	3–4	4	10
	Prolateral	1–4	2	5
	Retrolateral	0–3	0	11
Femur—	Dorsal ou.	0–1	1	10
	Dorsal mi.	1–4	3	9
	Dorsal in.	1	1	14
3—Meta.—	Ventral ou.	3	3	17
	Ventral in.	1–2	1	8
	Prolateral	2–3	2	13
Tibia—	Ventral ou.	2–4	3	8
	Prolateral	0–2	0	8
	Retrolateral	0–1	0	13
Femur—	Dorsal ou.	0	0	14
	Dorsal mi.	0–3	0	7
	Dorsal in.	1–2	1	12
4—Meta.—	Ventral ou.	1–2	1	9
	Ventral in.	2–3	2	13
Femur—	Dorsal mi.	1–3	2	7

Table 16. Spination of *Ariadna obscura*

		Female N = 2	
		Range	n
Palp	Patella	1	2
	Tibia	5	2
	Tarsus	8–9	1 ea.
Leg:			
1—Meta.—	Ventral ou.	6–7	1 ea.
	Ventral in.	5–6	1 ea.
	Prolateral	2	2
	Retrolateral	2	2
Tibia—	Ventral ou.	4	2
	Ventral in.	4	2
	Prolateral	4	2
	Retrolateral	4	2
Pat'l—	Prolateral	2	2
	Retrolateral	1	2
Femur—	Dorsal ou.	1	2
	Dorsal mi.	1	2
	Dorsal in.	2	2
	Prolateral	1	2
2—Meta.—	Ventral ou.	5–6	1 ea.
	Ventral in.	6–7	1 ea.
	Prolateral	2	2
	Retrolateral	2	2
Tibia—	Ventral ou.	4	2
	Ventral in.	1	2
	Prolateral	3	2
	Retrolateral	4	2
Pat'l—	Prolateral	2	2
Femur—	Dorsal ou.	1	2
	Dorsal mi.	1	2
	Dorsal in.	2	2
3—Meta.—	Ventral ou.	3	2
	Ventral in.	1	2
	Prolateral	3	2
	Retrolateral	2	2
Tibia—	Ventral ou.	3	2
	Prolateral	1	2
	Retrolateral	2–3	1 ea.
Femur—	Dorsal ou.	0–1	1 ea.
	Dorsal mi.	0	2
	Dorsal in.	1	2
4—Meta.—	Ventral ou.	1	2
	Ventral in.	2	2

Table 17. Spination of *Ariadna pilifera*

		Male N = 20–22			Female N = 71–80		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	22	0–1	0	72
	Tibia	0	0	22	2–6	4	41
	Tarsus	0	0	22	5–14	9	25
Leg:							
1—Meta.—	Ventral ou.	1–2	2	16	6–10	8	35
	Ventral in.	3–5	5	10	6–10	8	36
	Prolateral	0–1	1	13	0	0	71
Tibia—	Ventral ou.	4–6	5	12	3–7	4	41
	Ventral in.	0–2	1	8	3–7	4	46
	Ventral su.	0–1	1	18	0	0	72
	Prolateral	3–5	4	16	0–4	2	21
	Retrolateral	3–5	4	17	0–4	1	34
Femur—	Dorsal ou.	1–2	1	15	0–2	1	63
	Dorsal mi.	1–4	1, 2	8 ea.	0–3	1	52
	Dorsal in.	2	2	20	0–2	2	66
	Prolateral	0–1	1?	10	1	1	72
2—Meta.—	Ventral ou.	3–4	3	19	7–11	8	34
	Ventral in.	3–4	3	20	7–11	9	27
	Prolateral	0–1	0	15	0	0	71
	Retrolateral	0–2	1	12	0	0	71
Tibia—	Ventral ou.	4–7	5	10	4–7	4	48
	Ventral in.	0–2	2	12	1–3	2	40
	Ventral su.	0–1	1	20	0	0	72
	Prolateral	2–5	4	10	0–5	3	38
	Retrolateral	3–4	4	17	0–1	0	69
Femur—	Dorsal ou.	1–2	1	12	0–3	1	29
	Dorsal mi.	1–4	1	8	0–3	1	55
	Dorsal in.	1–3	2	17	1–3	2	63
3—Meta.—	Ventral ou.	3	3	21	3–4	3	75
	Ventral in.	0–2	2	18	1–2	2	71
	Prolateral	2–4	3	16	1–5	3	58
Tibia—	Ventral ou.	3–5	3	13	1–5	3	44
	Prolateral	2–4	3	12	0–4	2	34
Femur—	Dorsal ou.	0–1	0	19	0–1	0	69
	Dorsal mi.	0–4	3	8	0–2	0	32
	Dorsal in.	1–3	2	17	1–3	2	66
4—Meta.—	Ventral ou.	0–2	2	18	1–3	2	63
	Ventral in.	2–4	4	12	3–5	3	49
Tibia—	Ventral ou.	0–1	1	18	0–1	1	52
	Retrolateral	0	0	22	0–3	0	58
Femur—	Dorsal ou.	0	0	22	0	0	77
	Dorsal mi.	2–6	4	7	0–2	0	39
	Dorsal in.	0–3	1	10	0–2	0	55
	Retrolateral	0	0	22	0–4	0	32

TABLE 18. SPINATION OF *ARIADNA PRAGMATICA*

		Female N = 4–6		
		Range	Mode	n
Palp	Patella	0	0	6
	Tibia	2–4	3	3
	Tarsus	7–9	9	3
Leg:				
1—Meta.—	Ventral ou.	7–8	7, 8	3 ea.
	Ventral in.	7–10	7, 8	2 ea.
Tibia—	Ventral ou.	4	4	6
	Ventral in.	4–5	4	4
Femur—	Dorsal ou.	0	0	6
	Dorsal mi.	0–1	0	4
	Dorsal in.	0–1	0, 1	3 ea.
	Prolateral	1	1	6
2—Meta.—	Ventral ou.	7–9	7, 8, 9	2 ea.
	Ventral in.	8–10	8	3
Tibia—	Ventral ou.	4	4	6
	Ventral in.	1–2	1, 2	3 ea.
	Prolateral	0–1	0, 1	3 ea.
Femur—	Dorsal in.	1	1	6
3—Meta.—	Ventral ou.	2–3	3	5
	Ventral in.	1–2	1	5
	Prolateral	1–2	2	5
Tibia—	Ventral ou.	1–4	3	3
	Prolateral	0–1	0	4
Femur—	Dorsal in.	1	1	6
4—Meta.—	Ventral ou.	1–3	1	4
	Ventral in.	2	2	6
Femur—	Dorsal ou.	0	0	6
	Dorsal mi.	0–1	0	4
	Dorsal in.	0	0	6

TABLE 19. SPINATION OF *ARIADNA SOLITARIA*

		Juvenile N = 1–2	
		Range	n
Palp	Patella	1	2
	Tibia	3–5	1 ea.
	Tarsus	6	2
Leg:			
1—Meta.—	Ventral ou.	7	1
	Ventral in.	7	1
Tibia—	Ventral ou.	4	1
	Ventral in.	4	1
	Ventral su.	1	1
	Prolateral	3	1
	Retrolateral	3	1
Femur—	Dorsal ou.	1	1
	Dorsal mi.	1	1
	Dorsal in.	2	1
	Prolateral	1	1
2—Meta.—	Ventrol ou.	6	2
	Ventral in.	7	2
Tibia—	Ventral ou.	4	2
	Ventral in.	4	2
	Prolateral	2–3	1 ea.
	Retrolateral	1	2
Femur—	Dorsal ou.	1	2
	Dorsal mi.	1	2
	Dorsal in.	1–2	1 ea.
3—Meta.—	Ventral ou.	3	2
	Ventral in.	1	22
	Prolateral	2	2
Tibia—	Ventral ou.	2	2
Femur—	Dorsal ou.	0–1	1 ea.
	Dorsal mi.	0	2
	Dorsal in.	2	2
4—Meta.—	Ventral ou.	2	2
	Ventral in.	4	2

Table 20. Spination of *Ariadna tarsalis*

		Juvenile N = 6		
		Range	Mode	n
Palp	Patella	0	0	6
	Tibia	3–6	3	4
	Tarsus	6–9	6	3
Leg:				
1—Meta.—	Ventral ou.	8–9	9	4
	Ventral in.	8–9	8	5
Tibia—	Ventral ou.	5–9	5, 9	2 ea.
	Ventral in.	4–7	7	2
	Prolateral	0–3	2	3
	Retrolateral	0–3	3	4
Femur—	Dorsal ou.	0–1	1	4
	Dorsal mi.	0–2	1	4
	Dorsal in.	0–2	1	4
	Prolateral	1	1	6
2—Meta.—	Ventral ou.	8–9	8	5
	Ventral in.	7–10	9	3
Tibia—	Ventral ou.	6–11	7	2
	Ventral in.	4–6	4	3
	Prolateral	0–2	0	3
Femur—	Dorsal ou.	0–1	0, 1	3 ea.
	Dorsal mi.	1–2	1, 2	3 ea.
	Dorsal in.	1–2	1, 2	3 ea.
3—Meta.—	Ventral ou.	3	3	6
	Ventral in.	1–2	1	4
	Prolateral	2–3	3	4
Tibia—	Ventral ou.	3	3	6
	Prolateral	0–1	0	5
Femur—	Dorsal ou.	0	0	6
	Dorsal mi.	0–2	0	4
	Dorsal in.	1–2	1	4
4—Meta.—	Ventral ou.	1	1	6
	Ventral in.	2–3	2	5

Table 21. Spination of *Ariadna tovarensis*

		Female N = 4		
		Range	Mode	n
Palp	Patella	1	1	4
	Tibia	5–6	5, 6	2 ea.
	Tarsus	7–10	10	2
Leg:				
1—Meta.—	Ventral ou.	5–7	5	2
	Ventral in.	5–7	7	2
Tibia—	Ventral ou.	4	4	4
	Ventral in.	4	4	4
	Prolateral	3–4	3	3
	Retrolateral	4	4	4
Femur—	Dorsal ou.	1	1	4
	Dorsal mi.	1	1	4
	Dorsal in.	1–2	2	3
	Prolateral	1	1	4
2—Meta.—	Ventral ou.	5–7	5	2
	Ventral in.	3–5	5	3
Tibia—	Ventral ou.	4	4	4
	Ventral in.	3	4	4
	Prolateral	2–3	3	3
	Retrolateral	2–3	2	3
Femur—	Dorsal ou.	1	1	4
	Dorsal mi.	0–1	1	3
	Dorsal in.	1–2	1, 2	2 ea.
3—Meta.—	Ventral ou.	33	3	4
	Ventral in.	1	1	4
	Prolateral	1	1	4
Tibia—	Ventral ou.	1–3	3	2
	Prolateral	0–1	0, 1	2 ea.
Femur—	Dorsal in.	0–1	0, 1	2 ea.
4—Meta.—	Ventral ou.	0	0	4
	Ventral in.	4	4	4

TABLE 22. SPINATION OF *ARIADNA TUBICOLA*

		Juvenile N = 4		
		Range	Mode	n
Palp	Patella	1	1	4
	Tibia	5–7	7	2
	Tarsus	8–9	9	3
Leg:				
1—Meta.—	Ventral ou.	5–6	5	3
	Ventral in.	6	6	4
Tibia—	Ventral ou.	5–6	5, 6	2 ea.
	Ventral in.	5–7	6	2
	Prolateral	1–2	2	3
	Retrolateral	0–1	1	3
Femur—	Dorsal ou.	0	0	4
	Dorsal mi.	0–1	1	3
	Dorsal in.	0	0	4
	Prolateral	1	1	4
2—Meta.—	Ventral ou.	3–5	4	2
	Ventral in.	5–6	6	3
Tibia—	Ventral ou.	5–7	7	3
	Ventral in.	4–6	4	2
	Prolateral	2	2	4
Femur—	Dorsal ou.	0	0	4
	Dorsal mi.	0–1	1	3
	Dorsal in.	0	0	4
3—Meta.—	Ventral ou.	3	3	4
	Ventral in.	0	0	4
	Prolateral	0–1	1	3
Tibia—	Ventral ou.	1–2	1, 2	2 ea.
	Prolateral	0–1	0, 1	2 ea.
Femur—	Dorsal mi.	0–1	0	3
4—Meta.—	Ventral ou.	0	0	4
	Ventral in.	4–5	5	3

Table 23. Spination of *Ariadna weaveri*

		Male N = 3–4			Female N = 13–14		
		Range	Mode	n	Range	Mode	n
Palp	Patella	0	0	14	0	0	14
	Tibia	0	0	4	3–9	3	9
	Tarsus	0	0	4	6–15	12	4
Leg:							
1—Meta.—Ventral ou.		0	0	3	7–10	8, 9	5 ea.
Ventral in.		0	0	3	7–9	8	7
Tibia—Ventral ou.		4–5	5	2	4–5	4	11
Ventral in.		2	2	3	3–5	4	10
Ventral su.		0–1	0	2	0	0	14
Prolateral		1, 3, 4		1 ea.	0	0	14
Retrolateral		3–4	3	2	0	0	14
Femur—Dorsal ou.		0	0	3	0	0	14
Dorsal mi.		0–1	1	2	0–1	0	12
Dorsal in.		2	2	3	0–1	0	8
Prolateral		1	1	3	1	1	14
2—Meta.—Ventral ou.		0	0	4	7–11	7, 9	5 ea.
Ventral in.		0	0	4	9–16	10	5
Tibia—Ventral ou.		4	4	4	4–6	4	6
Ventral in.		1–2	1	3	1–4	2	9
Prolateral		1–4	1	2	0–1	0	12
Retrolateral		0–1	0, 1	2 ea.	0	0	13
Femur—Dorsal ou.		0	0	4	0	0	13
Dorsal mi.		0–1	0, 1	2 ea.	0	0	13
Dorsal in.		1–2	1	3	1–2	1	8
3—Meta.—Ventral ou.		3	3	4	3–4	3	13
Ventral in.		1	1	4	1–2	2	11
Prolateral		0	0	4	0–3	2	8
Tibia—Ventral ou.		1–2	2	3	1–3	2	12
Prolateral		0–1	0	3	0–2	1, 2	5 ea.
Femur—Dorsal ou.		0	0	4	0	0	14
Dorsal mi.		0	0	4	0	0	14
Dorsal in.		0–1	0, 1	2 ea.	1–2	1	12
4—Meta.—Ventral ou.		1–2	1	3	1–2	1	13
Ventral in.		3	3	4	3	3	14
Ventral su.		0–1	0, 1	2 ea.	0	0	14
Femur—Dorsal ou.		0	0	4	0	0	14
Dorsal mi.		2–3	2	3	0	0	14
Dorsal in.		0	0	4	0	0	14

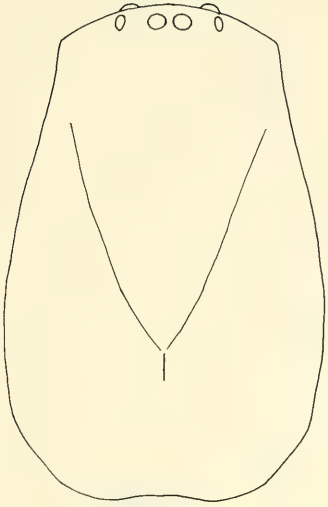
TABLE 24. DIAGNOSTIC FEATURES OF HAPLOGYNE SPIDER FAMILIES

	Plectreuridae	Diguetidae	Sicariidae	Scytodidae
Chelicerae	Joined basally; laminate, chelate.	Joined basally; laminate, chelate.	Joined basally; laminate, chelate.	Joined basally; laminate, chelate.
Colulus	Minute plate bearing 2 setae.	Tiny, conical, with 2 lateral setae.	Conspicuous, conical, with about 12 setae.	Conspicuous, conical or rounded, with 11–20 setae.
Male palp	Short tarsus, large bulb; embolus slender, simple, or flat, two-parted; no conductor	Short tarsus, large bulb; slender simple embolus; large scoop-like conductor.	Tarsus and bulb small; embolus conical basally, slender and simple distally; no conductor.	Tarsus variable, bulb large or small; embolus conical basally, slender and simple distally; no conductor.
Female genitalia	With bursa copulatrix; no sclerotized seminal receptacles.	With bursa copulatrix; a single median seminal receptacle.	?	No bursa copulatrix; a pair of seminal receptacles, these sometimes united.
Heart ostia	?	?	3 pairs	3 pairs
Anterior respiratory organs	Lungs	Lungs	Lungs	Lungs
Posterior respiratory organs	Median tracheal spiracle behind middle of abdomen; tracheae probably rudimentary.	Median tracheal spiracle behind middle of abdomen; tracheae simple, restricted to abdomen.	Median tracheal spiracle behind middle of abdomen; tracheae lost.	Median tracheal spiracle behind middle of abdomen; tracheae simple, restricted to abdomen.

Table 25. Diagnostic Features of Haplogyne Spider Families (*Continued*)

	Dysderinae	Segestriinae	Oonopidae	Caponiidae
Chelicerae	Free, subchelate, not laminate.	Free, subchelate, not laminate.	Free, subchelate, not laminate.	Free, subchelate, not laminate.
Colulus	Absent, or a tiny plate with 2–4 setae.	Large, rounded, with several setae.	Absent, or a tiny plate with 2 setae.	Absent.
Male palp	Variable, similar to segestriines or partly subdivided apically into several projections	Tarsus short or long, bulb large; embolus conical basally, slender and simple distally; no conductor.	Tarsus small; bulb large and globular with variable embolus, or no separate bulb; no conductor.	Tarsus short, bulb globular, embolus short to very long, curved, bifurcate at tip; no conductor.
Female genitalia	With copulatory bursa; T-shaped median seminal receptacle.	With copulatory bursa; tiny median seminal receptacle.	?	?
Heart ostia	2 pairs	2 pairs	2 pairs	2 pairs
Anterior respiratory organs	Lungs	Lungs	Greatly reduced lungs, or tracheae only.	Tracheae.
Posterior respiratory organs	Pair of tracheal spiracles just behind epigastric groove; tracheae well-developed, entering cephalothorax.	Pair of tracheal spiracles just behind epigastric groove; tracheae well-developed, entering cephalothorax.	Pair of tracheal spiracles just behind epigastric groove; tracheae well-developed, entering cephalothorax.	Pair of tracheal spiracles just behind epigastric groove; tracheae well-developed, entering cephalothorax.

Plate I. Fig. 1. *Ariadna mollis* (Holmberg). Dorsal view of female from Cavinna, Parana, Brazil. Fig. 2. *Ariadna maxima* (Nicolet). Sternum, endites, labium, and labrum of female from Mas Afuera Island, Juan Fernandez Islands, Chile. Fig. 3. *Ariadna boesenbergii* Keyserling. Ventral view of tibia II of female lectoparatype from Montevideo, Uruguay. Figs. 4, 6. *Ariadna boliviana* Simon. 4. Lateral view of carapace of male lectotype from Espíritu Santo, Bolivia. 6. Lateral view of carapace of female lectoparatype from Espíritu Santo, Bolivia. Fig. 5. Dorsal view of eye region of female *Ariadna sp.*, showing lines along which measurements were made. Fig. 7. *Ariadna gracilis* Vellard. Mesal view of femur I of female from St. André, Marajão, Brazil.



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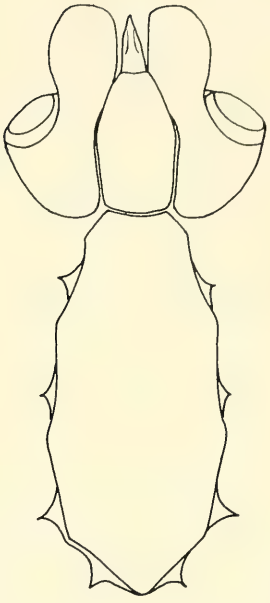

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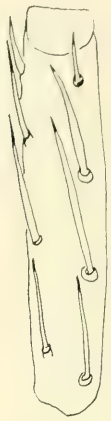

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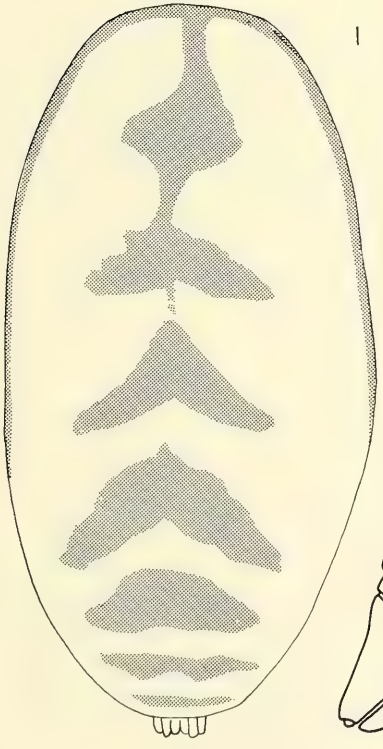

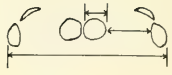

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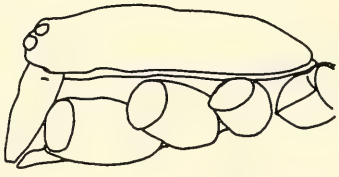

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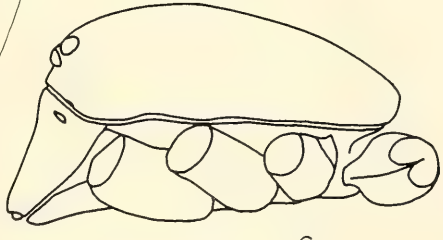

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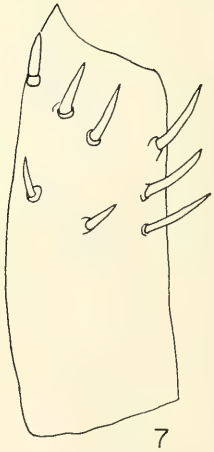

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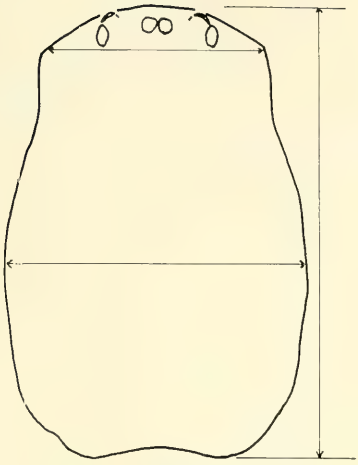
Plate II. Figs. 8–9. *Ariadna arthuri* Petrunkevitch. Female from South Bimini, Bahama Islands, showing lines along which measurements were made. 8. Dorsal view of carapace. 9. Ventral surface of cephalothorax. Fig. 10. *Ariadna fidicina* (Chamberlin). Dorsal view of carapace of female from Laguna Beach, California, showing stridulating grooves. Fig. 11. *Ariadna cephalotes* Simon. Ventral view of abdomen of female lectotype from San Mateo, Bolivia. Fig. 12. Left palp of male *Ariadna*, showing regions of palpal organ. A, bulb; B, midpiece; C, embolic portion. Fig. 13. Ventro-lateral view of metatarsus I of female *Ariadna*, showing one of the rows of ventral spines. Fig. 14. *Ariadna boliviana* Simon. Ventral view of genital region of female lectoparatype from Espíritu Santo, Bolivia. Overlying tissue removed to expose seminal receptacle. Fig. 15. Lateral view of leg I of *Ariadna sp.*, showing lines along which measurements were made.



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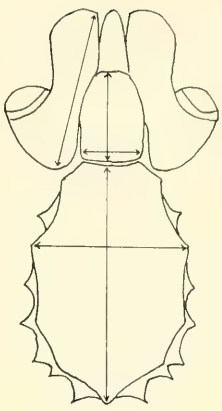

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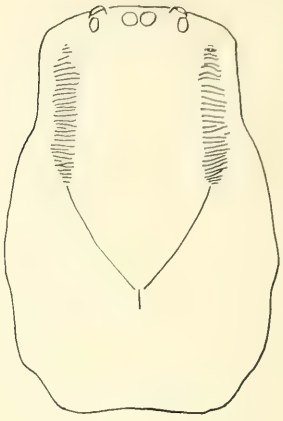

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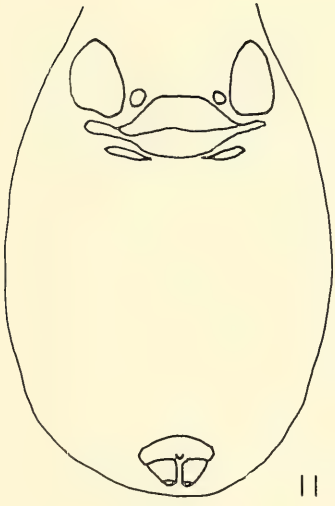

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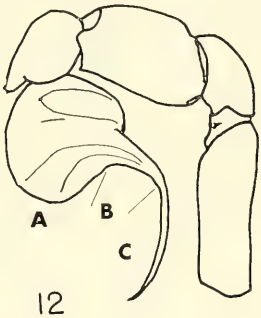

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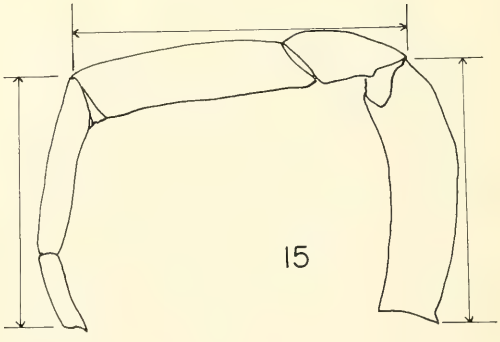

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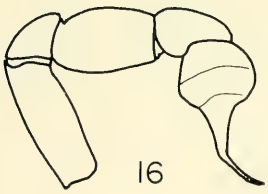
Plate III. Figs. 16–17, 22. *Ariadna mollis* (Holmberg). Male from Tigre, Buenos Aires, Argentina. 16. Left palp, mesal view. 17. Left palp, lateral view. 22. Tibia and metatarsus I, dorsal view. Figs. 18–19, 21. *Ariadna maxima* (Nicolet). Male from Mas Afuera Island, Juan Fernandez Islands, Chile 18. Left palp, lateral view. 19. Left palp, mesal view. 21. Tibia and metatarsus I, dorsal view. Fig. 20. *Ariadna pilifera* O. P. Cambridge. Tibia and metatarsus I of male, dorsal view. (Holotype of *Ariadna acanthopus* Simon from Guanajuato, Mexico.) Figs. 23–25. *Ariadna isthmica* sp. n. Male holotype from Barro Colorado Island, Canal Zone, Panama. 23. Tibia and metatarsus I, dorsal view. 24. Left palp, mesal view. 25. Left palp, lateral view.



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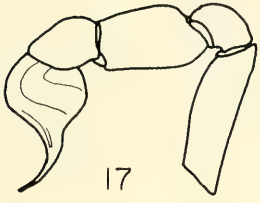

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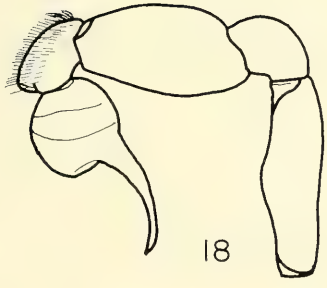

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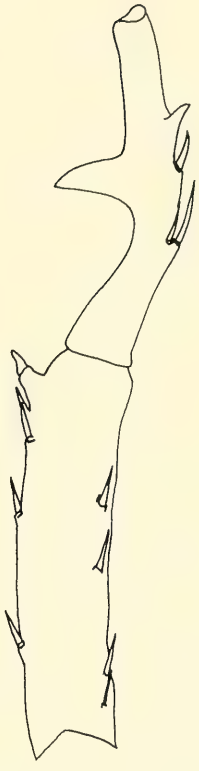

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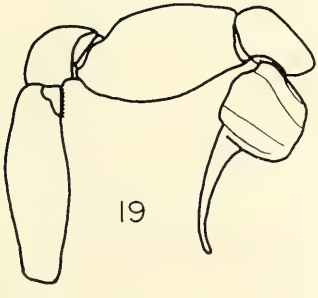

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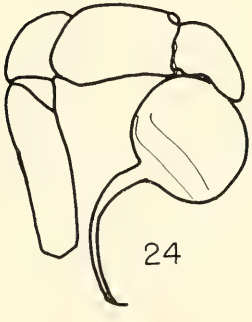

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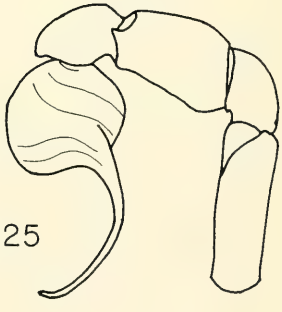

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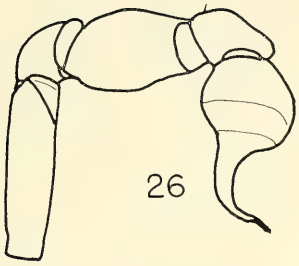
Plate IV. Figs. 26–27, 32. *Ariadna arthuri* Petrunkevitch. Male from South Bimini, Bahama Islands. 26. Left palp, mesal view. 27. Left palp, lateral view. 32. Tibia, metatarsus, and tarsus I, dorsal view. Figs. 28–29, 33. *Ariadna gracilis* Vellard. Male from Téfé, Amazonas, Brazil. 28. Left palp, lateral view. 29. Left palp, mesal view. 33. Left tibia and metatarsus I, dorsal view. Fig. 30. *Ariadna isthmica* sp. n. Male from Barro Colorado Island, Canal Zone, Panama. Left metatarsus and tarsus IV showing scopulae. Fig. 31. *Ariadna pilifera* O. P.-Cambridge. Female from Southwestern Research Station, 5 mi W of Portal, Cochise Co., Arizona. Ventral view of metatarsus IV showing comb and outer row of ventral spines.



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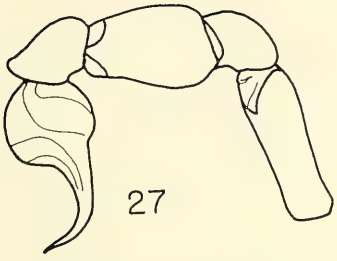

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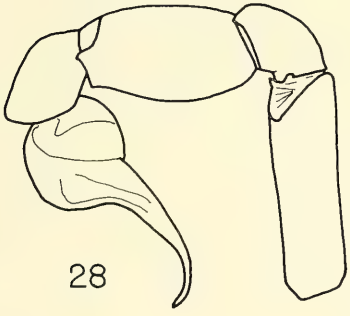

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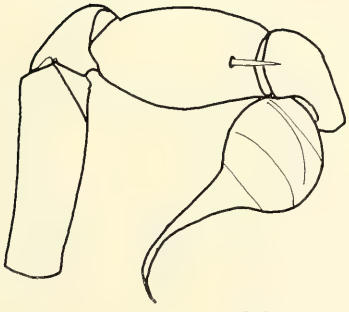

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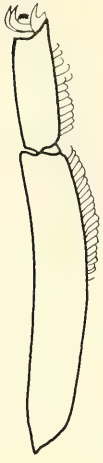

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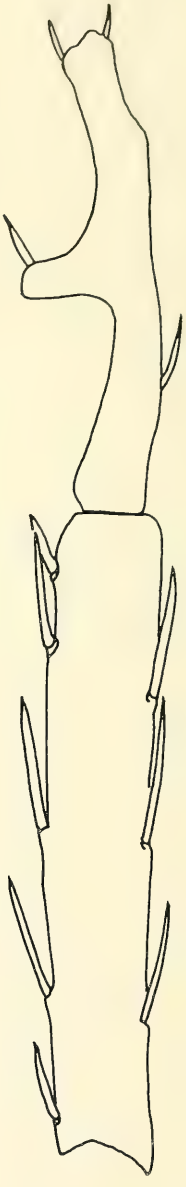

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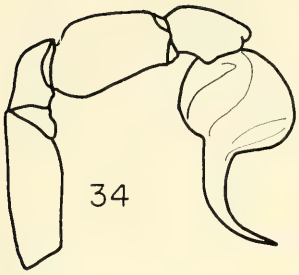
Plate V. Figs. 34–35, 39. *Ariadna peruviana* sp. n. Male from Lima, Lima, Peru. 34. Left palp, mesal view. 35. Left palp, lateral view. 39. Left tibia and metatarsus I, dorsal view. Figs. 36–37, 40–41. *Ariadna pilifera* O. P. Cambridge. Male from Southwestern Research Station, 5 mi W of Portal, Cochise Co., Arizona. 36. Left palp, lateral view. 37. Left palp, mesal view. 40. Left tibia I, lateral view. 41. Left tibia, metatarsus, and tarsus I, dorsal view. Figs. 38, 42–43. *Ariadna bicolor* (Hentz). Male from Mohican State Park, Ashland Co., Ohio. 38. Left tibia and metatarsus I, dorsal view. 42. Left palp, mesal view. 43. Left palp, lateral view.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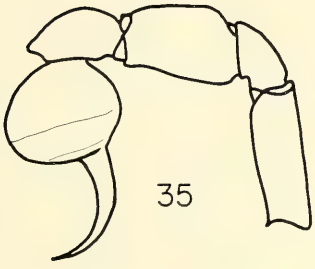
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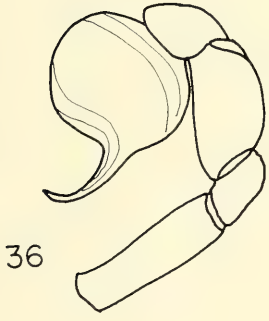
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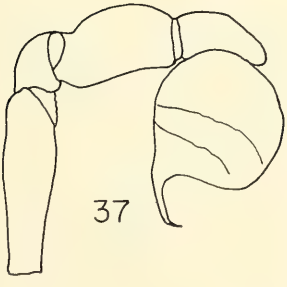
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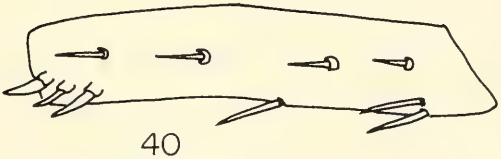
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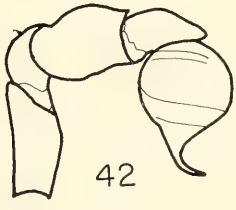
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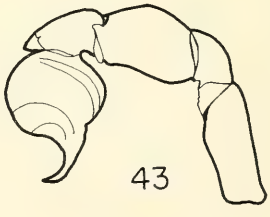
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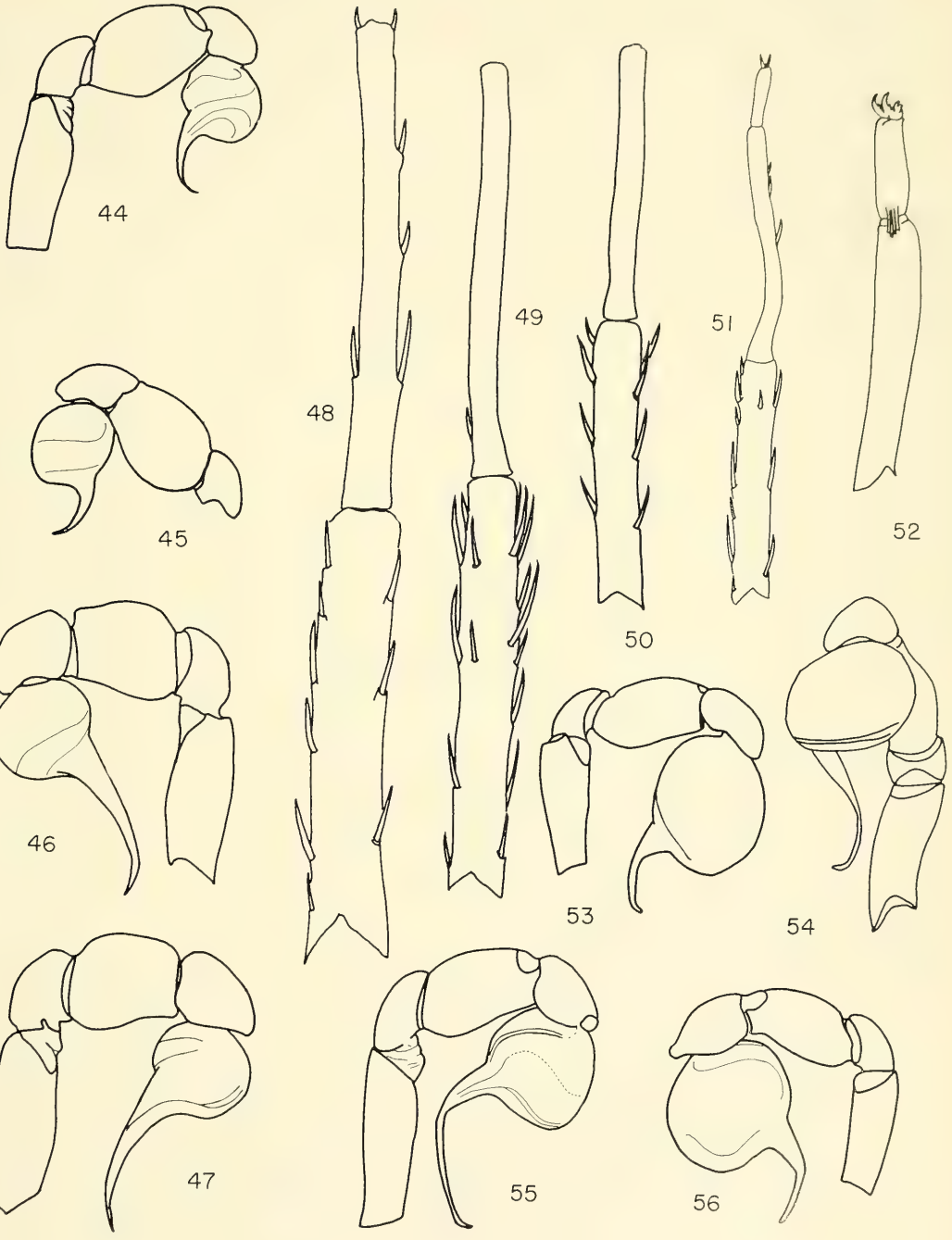
Plate VI. Figs. 44– 45, 49. *Ariadna caerulea* Keyserling. Male from Sierra Nevada de Santa Marta, Magdalena, Colombia. 44. Left palp, mesal view. 45. Left palp, lateral view. 49. Left tibia and metatarsus I, dorsal view. Figs. 46–48. *Ariadna boesenbergii* Keyserling. Male lectotype from Montevideo, Uruguay. 46. Left palp, lateral view. 47. Left palp, mesal view. 48. Left tibia and metatarsus I, dorsal view. Figs. 50, 53, 56. *Ariadna weaveri* sp. n. Male from Clarion Island, Revilla Gigedo Islands group, Mexico. 50. Left tibia and metatarsus I, dorsal view. 53. Left palp, mesal view. 56. Left palp, lateral view. Figs. 51–52, 54–55. *Ariadna boliviana* Simon. Male lectotype from Espíritu Santo, Bolivia. 51. Left tibia, metatarsus, and tarsus I, dorsal view. 52. Right metatarsus and tarsus IV, showing comb. 54. Left palp, anterior view. 55. Left palp, mesal view.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